SPATIAL COUPLING OF PLANT RECRUITMENT PROCESSES; VEGETATION CHANGE AND THE REGENERATION ECOLOGY OF HOON HAY VALLEY, PORT HILLS, CANTERBURY, NEW ZEALAND

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"Though I do not believe that a plant will spring up where no seed has been, I have great faith in a seed. Convince me that you have a seed there, and I am prepared to expect wonders."

Henry D. Thoreau (1817 - 1862)

ABSTRACT

Spatial coupling of plant recruitment processes was measured during 1996 in a dynamic post-agricultural successional environment on the Port Hills of Banks Peninsula. Steps along a conceptual vegetation→seed rain→seedlings recruitment continuum were measured, and the degree of spatial coupling (as measured by correlations of DCA ordination axis position) between each determined. Spatial coupling of recruitment processes provides a direct measure of potential vegetation change; tight coupling indicates vegetation is changing little as each recruitment step is spatially similar to the step previous, whereas weak coupling indicates dynamic change as steps are not spatially related. Coupling was weakest at the vegetation→seed rain and seed rain→seedlings stages, indicating that at these stages plant dispersal and vegetation change are most strongly expressed. Coupling was strongest at the vegetation→seedling stage, indicating that processes associated with seedling establishment and survival offer the strongest impediments to vegetation change. Coupling of all steps was weakest at the habitat-type level, with spatial patterns related to presumed successional age, indicating that vegetation change is proceeding in a process of within-valley succession and species migration. This result confirms those of previous studies which have investigated vegetation change on the Port Hills and Banks Peninsula. It indicates that with the removal of proximate causes of disturbance (fire, grazing, agriculture, etc.) the overwhelming trend of vegetation change in post-agricultural successional environments such as this is toward forest dominated by native species.

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CHAPTER 1

INTRODUCTION

To walk through any part of the New Zealand landscape which is easily accessible is to experience a landscape which owes more to the actions of human settlement than it does to any 'natural' ecology. Several short centuries of human occupation have left their indelible imprint on the ecology of lowland New Zealand to the point where essentially all the easily accessible land has been converted to 'productive' use, and is as modified as any landscape in the world. As Park (1995) describes, the full consequence of this "total, deliberate extermination from New Zealand's plains" has never been really been grasped. When the smoke of the colonists fires cleared in the early twentieth century New Zealand had become a different country. In only a few decades the earliest European settlers had turned what was predominantly a forested landscape into one where 'natural' landscapes are confined to places too cold, too wet, or too inaccessible to offer any potential for 'productive' use. This massive alteration of ecosystems had however begun centuries before the arrival of European settlers as the first wave of human settlement arrived from Polynesia. The first centuries of Maori settlement of New Zealand were characterised by resource wastage and species extinction on a scale relative to that of later European settlement. More bird species became extinct between the arrival of Polynesian settlers and the first European contact than have gone extinct since, including the 27 species of an entire order (Dinorthiformes, the moas) (Holdaway 1989, Bell 1991). Fires associated with early Maori settlement throughout New Zealand razed enormous areas of forest, although nowhere near as much as was cleared converting forest to pasture.

Human settlers brought with them, to turn a Biblical analogy on its head, an 'anti-Ark' of exotic species which have decimated the indigenous flora and fauna and insidiously continue to infiltrate and wreck havoc among the remaining 'natural' ecosystems. Mention of possums immediately brings to mind images of forest destruction and ecosystem decline. As Park (1995) says human settlement has banished nature from the lowlands and no more does one find the spirit of the land in what the poet Charles Brasch called "the savage forests that from the groins and armpits of the hills do fiercely look" ('The Silent Land'). The reality of this stares us full in the face in lowland New Zealand; a drive across the Canterbury Plains yields little evidence of native species, and it requires a leap of imagination to visualise the vibrant and dynamic ecosystems which would have blanketed the land prior to human settlement.

The last few decades have seen a growing realisation of the limits of the natural world and the scale of the negative effects that human technological endeavour has had on it (e.g. Suzuki 1993, Litvinoff 1990). There has been a growing desire among many to redress environmental wrongs and try and stem the tide of environmental degradation. Accompanying this desire is an upsurge of interest and advances in techniques of ecological restoration by which this can be achieved. In its broadest sense ecological restoration provides the opportunity to return an ecosystem to a state approaching that which would have been present prior to human intervention or disturbance (National Research Council 1991).

There is a burgeoning literature on restoration discussing at length what it is, how it works, techniques by which it might be achieved, and ethical and moral considerations surrounding its use. Restoration means different things to different people, and has been given a number of different and generally synonymous names including rehabilitation, reallocation, reconstruction, re-creation (Hobbs and Norton 1996). Restoration constitutes a continuum from a essentially non-interventionist management of relatively un-modified sites (e.g. removing browsing stock from a forest remnant), through to complete rebuilding of ecosystems following total devastation such as after open cast mining. Although the goals and techniques used in each restoration project differ, the approach of each is fundamentally similar. To paraphrase Hobbs and Norton (1996), the aim of restoration (explicitly stated or otherwise) is to return a system degraded in some way by human activity to one which is protective, productive, aesthetically pleasing, or valuable in a conservation sense. Hobbs and Norton (1996) identify key processes which they consider essential to the successful integration of restoration into land management at the landscape level, namely

- Identify the processes leading to ecosystem degradation or decline
- Develop models to reverse or ameliorate the degradation or decline
- Determine realistic goals for re-establishing species/functional ecosystems, recognising both the ecological limitations on restoration, and the socio-economic and cultural barriers to its implementation
- Develop easily observable measures of success
- Develop methods for implementing these restoration goals at a scale commensurate with the restoration problem
- Formulate these methods for inclusion in land-use planning and management strategies
- Monitor key system variables, assess progress of restoration relative to agreed goals, and adjust procedures as necessary.

Hobbs and Norton (1996) suggest that restoration activities frequently occur with little or no consideration of these processes. They emphasise the importance of a function-and-process approach, for as Reay (1996) asserts if restoration is to have any substantial conservation benefit it must go beyond simple structural and compositional reconstruction and restore biological interactions, processes and integrity (Ewel 1987, Andersen 1993).

Ecological function and process extend from relatively fine scale phenomena such as seed germination, individual plant growth, competition, and herbivory (e.g. Janzen 1970, Harper 1977 Fenner 1985, Silvertown 1987, Tilman 1988), to large and complex biogeochemical functions of mineral cycling, water cycles, and global atmospheric processes (Barbour *et al.* 1987). In order to effectively achieve ecosystem restoration with the processes listed above it is necessary to study and understand ecosystem functions and processes firstly in order to identify those which are of importance to restore 'healthy' ecosystems, and secondly to identify means by which these functions may be restored (Armstrong 1993).

In restoration of terrestrial ecosystems, which are the subject of the majority of restoration efforts to date (Hobbs and Norton 1996, Luken 1990, Jordan *et al.* 1987), a key ecological process is succession. Succession is the process by which ecosystems change (Burrows 1990). This change is generally in terms of species composition, and is brought about by processes of species expansion and decline associated with species migration, or processes of inter-specific competition between species already present at a site (e.g. Connell and Slatyer 1972). Succession and processes of vegetation change have been one of the major foci of plant ecology throughout its history, and are the subject of many excellent books and review articles (e.g. Burrows 1990, Tilman 1978, Miles 1979), a substantive review of which is beyond the scope of this study. Suffice to say that succession is about processes of vegetation change, and encompasses the interactions between plants, between plants and their environment, and increasingly between communities of plants and anthropogenic agents of ecosystem change (Burrows 1990). If one is interested in managing processes of vegetation change, as is the case in ecological restoration of terrestrial ecosystems, then study of succession has the potential to offer considerable insights as to how vegetation change can be enhanced such that restoration may be achieved.

Succession represents the interface between generations and so constitutes, in the words of Harper (1977), a keystone demographic bridge. Herrera *et al* (1994) state that with very few exceptions studies associated with this interface have fallen into one of three major categories, each corresponding to a consecutive step along a conceptual recruitment pathway from seed production → seed dispersal → seed rain → seed

germination → seedling establishment (Herrera *et al.* 1994). The first category are studies which focus on the dissemination of seeds, identifying dispersal agents and spatial and temporal patterns of fruit consumption without investigating its consequences. The second are studies investigating patterns of seed rain in space and time, and the third category are those demographically oriented studies investigating patterns of seed and seedling survival.

Very few studies have made any attempt to link these inter-related steps in a useful manner and cross Harper's 'demographic bridge', and the fact that this was the approach of Herrera *et al.* (1994) represents a considerable conceptual advancement in successional ecology. Herrera *et al.* (1994) linked population processes and vegetation change to the degree of coupling between patterns of seed dispersal, subsequent patterns of seed rain, and demographic processes at the seedling stage for a mast-seeding bird dispersed shrub in Mediterranean forest. In so doing they were able to identify processes which had particular implications for evolutionary processes, and for processes of vegetation change.

It does not take much to realise the potential benefits of this approach to studies of those processes and functions which are essential for successful restoration of terrestrial ecosystems. An assessment of the degree of coupling between successive steps along the conceptual seed production→seed dispersal→seed rain→seed germination→seedling establishment recruitment pathway can identify those processes which are impeding succession, and likewise suggest possible ways in which succession can be enhanced. In this respect the approach of Herrera *et al.* (1994) has formed the conceptual inspiration for this study.

Herrera *et al.* (1994) studied recruitment for a single species, and while this approach may produce detailed information it does little for integrating patterns of recruitment and vegetation change at a community level which would be of most use in restoration. This study takes the conceptual approach of Herrera *et al.* (1994) one step further by considering recruitment processes at a community level and identifying the degree of coupling between spatial patterns of seed production, seed rain, and seedling germination and establishment for a single reproductive event in a successional environment on the Port Hills.

The degree of coupling of spatial recruitment patterns offers key insights to processes of successional change. In the hypothetical situation where vegetation is not changing spatial patterns of vegetation, seed rain, and seedlings will be perfectly coupled; species will be represented in similar proportions at each step, ensuring that spatial expression of vegetation pattern remains static. If however vegetation is changing then coupling will

not be perfect, as species will be represented at each step along the conceptual recruitment pathway in differing amounts. Discontinuities in coupling represent the potential for species dispersal and successional change, and so investigation of successive steps along the conceptual recruitment pathway indicate factors which either enhance or retard vegetation change.

The objective of this thesis is thus to investigate the degree of coupling between spatial patterns of vegetation, seed rain, and seedling establishment for the successional vegetation of Hoon Hay valley. To this end the thesis consists of six further Chapters. Chapter 2 provides a description of the study site, including its location and physiognomy including geology, landforms, and soil pattern. The climate experienced by the valley is described, together with a brief history of its vegetation and land use and the effects that these have on present day vegetation. The following three chapters provide detailed investigations of the patterns- both spatial and temporal - of current vegetation (Chapter 3), seed rain (Chapter 4) and seedling populations (Chapter 5). Each of these three Chapters investigates a step on the conceptual recruitment pathway described above, and to this end can be considered as a separate entity. Chapter 6 then integrates each of the preceding chapters and presents a synthesis which enables assessment of the coupling of spatial patterns of the conceptual recruitment pathway. The implications that this coupling has for vegetation change within Hoon Hay Valley are discussed, together with the implications that this has for restoration of forested ecosystems on the Port Hills

CHAPTER 2

SITE DESCRIPTION

1. LOCATION

Hoon Hay Valley is one of a series of similar valleys on the north western flanks of the Port Hills of Banks Peninsula (NZMS M36 796325, 172° 37' E, 43° 37' S). The valley is defined to the north by Worsleys Spur, and to the south by Kenedy's Bush spur. Kennedy's Track, a popular recreational walking and mountain-biking track, joins the Summit Road at the top of the valley (Figure 2.1).

The study area is within the Port Hills Ecological District, which is part of the Banks Ecological Region (Wilson 1992). The main axis of the valley trends approximately north west, and the whole valley spans an altitudinal range from around 50m above sea level in the lower valley, to around 400m on the upper flanks; Marley's Hill at the north-eastern end of the valley is 502 m above sea level. There are several side valleys running off the main valley axis, and a small stream runs down the main valley which flows continuously in winter, but only infrequently during the drier months. The lower part of the valley is broad and flat, and is currently in farmland. The middle portion of the valley rises steeply through a narrow, steep-sided section until broadening out at an altitude of around 200 m to a basin just over 1 km across.

2. GEOLOGY AND LANDFORMS

The Port Hills are the western extension of Banks Peninsula. The Peninsula is the remains of lava flows and other volcanic products (tuffs, tephras, and pyroclastic flows etc.) of three large volcanoes, the eroded peaks of which now form Lyttleton and Akaroa harbours.

Weaver *et al.* (1985) provide an excellent and accessible account of the volcanic geology of Banks Peninsula and the Port Hills, which can be broadly summarised as follows. The oldest rocks on the Peninsula pre-date the volcanic activity and are found around Gebbies Pass, toward the southern end of the Port Hills. These rocks are part of the Torlesse Terrane on which the Southern Alps, the Marlborough ranges and the main ranges of the North Island are built. They are sedimentary in

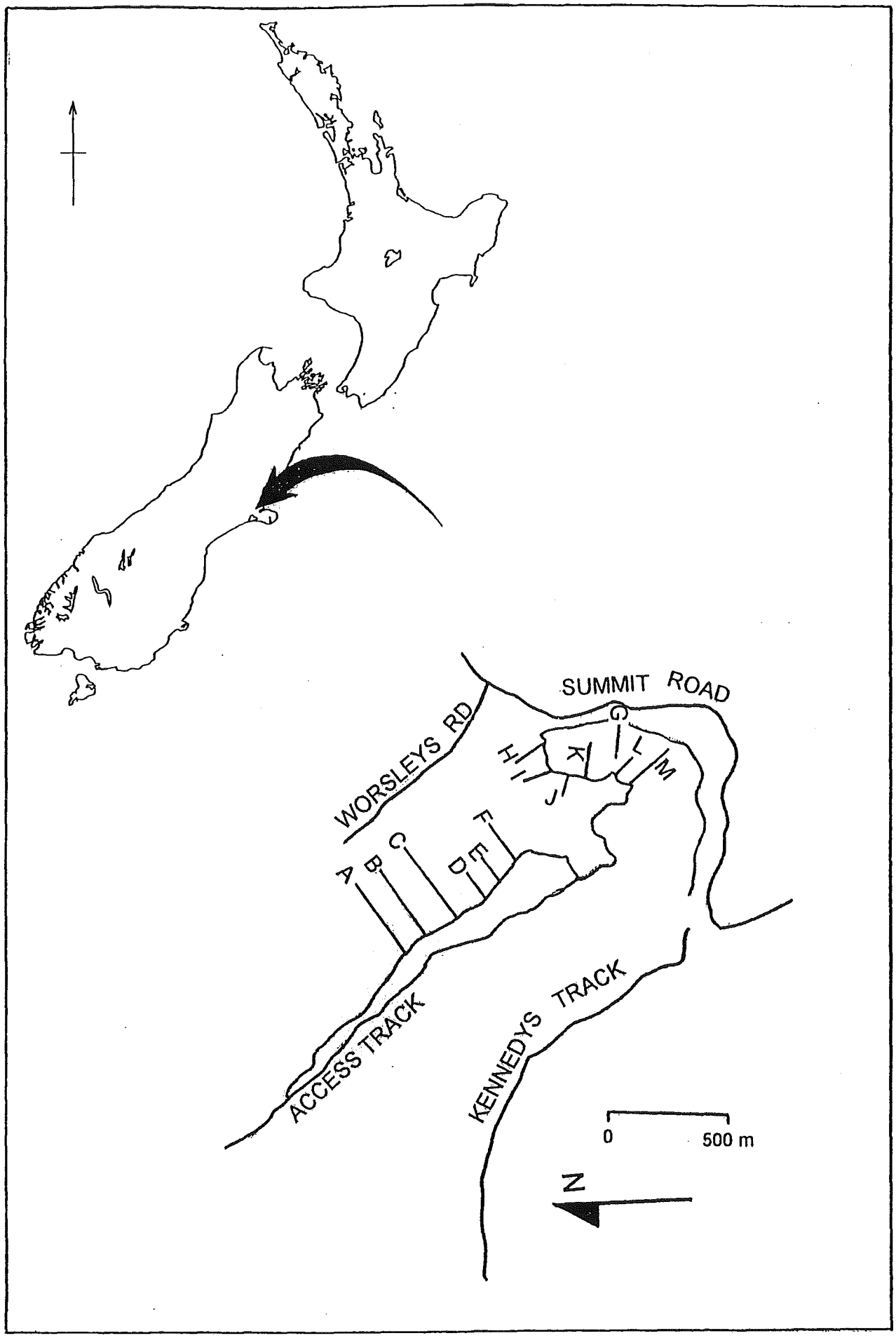

Figure 2.1. Location map, showing approximate location of Valley access tracks, and the survey transects described in Chapter 3.

origin, somewhere in the order of 240 million years old, and were submerged until about 15 million years ago. The oldest volcanic rocks on the Peninsula are considerable younger than this, and are also found in the Gebbies Pass area. They are approximately 90 million years old, and are part of a once extensive volcanic field now mostly removed by erosion.

Between this time and the volcanism which created most of the Peninsula, Banks Peninsula was submerged beneath the sea. Sedimentary deposits from this time are present around Chateris Bay and indicate that the Peninsula was still submerged 20 million years ago (MYA). Around 15 MYA the Kaikoura Orogeny began (the major period of uplift and land-building which gave rise to most of New Zealand's geology) and sedimentary Banks Peninsula emerged from beneath the sea. The period of volcanism which formed most of present-day Banks Peninsula began at about the same time. There were a series of eruptive events from several volcanic centres, most notably Governor's Bay (15 MYA), Lyttleton (12 MYA), Mt. Herbert (10 MYA) Akaroa (9 MYA) and several small eruptions around Diamond Harbour around 6 MYA.

Banks Peninsula was an island unconnected to the mainland until the glaciations of the last 2 million years. Land-bridges would have formed as sea levels fell at glacial maxima, and a permanent mainland connection was formed in the last glaciation which ended 10 - 14 000 years ago. Although glaciation did not affect the Peninsula directly, mainland glaciation had several implications for the Peninsula. Firstly the formation of a land-bridge allowed the migration of plant and animal species from the mainland to the Peninsula (Wilson 1992), and secondly glacial activity provided a source of fine eroded rock, which was blown from the mainland to the Peninsula to form a loess mantle, in places up to 20 m thick (Griffiths 1974, Fitzgerald 1966). It is also likely that periglacial conditions were experienced by the exposed peaks of the Peninsula, allowing the persistence and expansion of tussock grasslands (Wilson 1992).

3. SOILS

The soils in Hoon Hay valley form a mosaic related to weathered basalt regolith from volcanic deposits, primary loess from the Plains river valleys, and related colluvial complexes. Four broad groups (series) have been described, principally on the basis of initial mineral material and climate. In the sub-humid climate (at altitudes less than about 300 m) soils derived from a loess matrix are in the Takahe series, and those from basalt are the Cashmere series. Above 300 m loess soils form the Summit series, and basalt soils the Rapaki series. Inter-grades and complexes between these types have been

described and are common, with distribution of these depending primarily on topography (Griffiths 1974, Fitzgerald 1966).

All soils are well drained and will dry, often to wilting point, in summer. As described below there is an aspect relationship to rainfall, and so north facing slopes will dry faster than those facing south. Leaching will occur on sites with high rainfall, but because of the marked seasonality of soil moisture is unlikely to be a dominant pedogenic process. Fertility is medium to good, depending on parent material, with the brown granular loams of the basalt-derived Rapaki and Cashmere series enjoying substantially higher fertility than the loess-derived Yellow Brown Earths (Brown Soils in the revised New Zealand Soil classification of Hewitt (1992)) of the Takahe and Summit series (McClaren and Cameron 1990, Fitzgerald 1974, Griffiths 1966).

4. CLIMATE

Hoon Hay valley falls within in the Lowland bioclimatic zone of Wilson (1993a). The climate experienced by the valley differs in several ways from that experienced by the surrounding plains, due primarily to the maritime influence of Banks Peninsula and interactions of wind due to local topographic modification of prevailing synoptic airflows (Jayet 1986, Cullen 1996).

Cullen (1996) provides an excellent review of the climatology of Hoon Hay valley, which may be summarised as follows. The annual average temperature at Christchurch Airport is 11.6 °C, with a summer maximum in January and a winter minimum in July, and Cullen (1996) reports that the difference between temperatures in the valley and those recorded at Christchurch Airport is on average less than around 1 degree. However, altitude exerts a significant influence on temperatures within the valley, and the upper valley commonly experiences lower temperatures than the lower valley. Temperature inversions can occur during winter which reverse this trend and at times, dependant on conditions, the valley can experience significantly warmer temperatures than the adjacent plains (Cullen 1996).

The mean annual rainfall on the plains immediately adjacent to the Port Hills is generally less than 700 mm $yr.^{-1}$ (Jayet 1986). Several studies have measured rainfall on the Port Hills as being higher than this due to interactions of wind and altitude. For example Cullen (1996) investigated the pattern of precipitation in the valley, and reported that altitude is the most important controller of precipitation, with the upper and lower parts of the valley receiving 36% and 22% more precipitation than Christchurch airport respectively. This concurs with the observation of Griffiths (1974), who cited data reporting estimates of 760 mm $yr.^{-1}$ at the lower slopes and valley floor, ranging to

slightly over 1000 mm $yr.^{-1}$ at elevations over 300 m. Both authors report aspect and topographic effects which mediate precipitation, and as the majority of the rain-bearing winds are from the south-west (Jayet 1986), slopes with a south trending aspect receive more precipitation than those in the lee of the winds. Griffiths (1974) observed that precipitation was nearly as low on the Worsleys Spur as it was on the plains, although this is not supported by Cullen (1996). There is a mild seasonality to rainfall patterns with February being on average the driest month and July the wettest, although spring (September to November) is generally the driest season (Jayet 1986). Cullen (1996) reports that snow falls on average three times a year, with drifts can persist for several days. Altitude is the principle controller of soil moisture, with patterns similar to those recorded for precipitation (Cullen 1996).

The Southern Alps present a rain barrier to the rain-bearing westerly airflows which dominate the climate of the south Island (Jayet 1986). The Alps result in the formation of a lee pressure trough which produces a prevailing north/north easterly airflow on the coastal Canterbury Plains (Jayet 1986). In contrast Hoon Hay valley is dominated by a south easterly airflow, and Cullen (1996) attributes this difference to cold air drainage and channelling of airflow from surrounding topography. Anabatic (upslope) winds are commonly observed as a result of daytime heating.

Cullen (1996) engaged in a preliminary investigation of the light environment beneath the different vegetation types present in the valley, and it was observed that received photosynthetic photon flux density (PPFD - a measure of irradiance in the photosynthetically active waveband (400 - 700 nm)) in the 'forest' was between 10% and 32% of that experienced at open sites. A significantly higher PPFD was observed beneath 'scrub', and it was noted that both these values were higher than had been observed in similar studies in New Zealand (e.g. McDonald and Norton 1992).

5. VEGETATION HISTORY

Current vegetation on Banks Peninsula and the Port Hills is an artefact largely of human invention, and is representative of the highly modified predominantly agricultural landscape common throughout much of lowland New Zealand (Park 1995). In pre-human times the Canterbury Plains, Banks Peninsula and the Port Hills were a predominantly forested landscape (Molloy 1969, Molloy *et al.* 1963; , Wilson 1992). Evidence suggests that there was a virtually complete forest cover below the current altitudinal limits of forest distribution, and this evidence is in the form of relict pit and mound micro-topography (pits and mounds associated with tree windthrow) (Wilson

1992), soil profile forms more commonly associated with forest vegetation, and logs in areas currently lacking forest cover (e.g. Petrie 1963).

The forests which would have been present probably varied significantly with location, and the Port Hills would most likely have supported a mixed angiosperm/podocarp association. The podocarp species present would most likely have been *Podocarpus totara*, with *Podocarpus hallii* on higher altitude sites, together with matai (*Prumnopitys taxifolia*) and kahikatea (*Dacrycarpus dacrydioides*), with their distribution depending on factors such as soil properties and local climate (Wilson 1992). Miro (*Prumnopitys ferruginea*) may have been present but was probably quite uncommon and confined largely to the port Levy and Pigeon Bay area (D. A. Norton, pers. comm.). Angiosperm species would have been the most abundant forest species. Beech (*Nothofagus*) would have been more abundant during the colder and drier conditions of the last glaciation, probably migrating from the mainland mountain across land bridges formed during successive periods of glacial advance (Wilson 1992). Beech is now largely absent from the Peninsula, being confined to cooler and wetter parts of the south-eastern corner of the Peninsula (Wardle 1984).

The first human settlement of New Zealand occurred sometime between 900 and 1000 years ago (Salmon 1975), although there is some evidence that there was human contact considerably earlier than this (Sharp 1956, Wardle 1984), and McCulloch (1987, in Wilson 1992) suggests that a thousand years of human occupation of Banks Peninsula is a reasonable assumption. As in many areas of New Zealand, the arrival of the first Polynesians had significant impacts on the forest and ecology of Banks Peninsula and the Port Hills. One of the most significant and widely reported phenomena associated with Polynesian settlement was the advent of large scale forest clearance by fire. Sub-fossil charcoal is common in buried soil profiles throughout the eastern South Island, as it is over large areas of lowland New Zealand (Molloy *et al.* 1963), and analysis of these charcoal deposits by radiocarbon dating techniques (among others) has indicated that the majority of fires occurred between 1000 and 500 years ago (Molloy *et al.* 1963.). More recent work (Burrows 1996a) has indicated that some of the charcoal deposits are associated with fires which occurred substantially prior to this however, probably associated with natural ignition during drier climatic periods.

Fires associated with Polynesian settlement resulted in large areas of forest being cleared, and it has been estimated that up to half the pre-human forest cover had been cleared by fire by the arrival of the first European settlers in the 18th and 19th centuries (Wardle 1984). Not all of this fire would have been as a direct result of human activity (Burrows 1996a), but a significant proportion would have been. Several reasons for large scale fire have been postulated, although the early suggestion that fire was used as a large scale

moa-hunting tool has largely been debunked (McGlone 1989). More reasonably explanations include forest clearance for shifting agriculture (bracken root was an important food source which grew particularly well on recently burned land), defence, clearance of transport routes, and accidental fires associated with areas of settled habitation (McGlone 1989, Wilson 1992). On Banks Peninsula fire was apparently confined largely to ridge crests (supporting the transport route clearance idea) and areas immediately surrounding settlement sites, and by the arrival of the first European settlers roughly one third of the original forest cover would have been removed. With forest clearance tussock grasses which would previously been confined to rocky outcrops and drier ridge crests expanded their distribution, such that the anthropogenic grasslands which would have greeted the early European colonialists on parts of the Peninsula would have been present for several centuries (Wilson 1992).

The second significant implication of Maori settlement was in the extinction and introduction of species. Prior to Maori arrival the were no land based carnivorous mammals present in New Zealand, and as a result the native fauna had evolved no defences to such animals, and were particularly susceptible to any introductions. The early Maori immigrants brought with them dogs (*Canis familiaris*, kuri) and rats (*Rattus exulans*, kiore), which would have found many of the bird species easy prey. Maori also had a direct hand in the extinction of several bird species, most notably the 27 species of moa (*Dinorthiformes* spp.) which became extinct within the first few centuries of habitation as a result of either hunting pressure or predation by introduced animals. Evidence from sub-fossil remains and midden sites has indicated that somewhere around 50 species of bird and lizard were driven to extinction following the arrival of the first Polynesian settlers, with a further 9 bird species becoming extinct since European settlement (Bell 1991, Towns and Dougherty 1994)

In spite of these significant perturbations the landscape of Banks Peninsula was still largely forested on the arrival of the first European settlers to Canterbury. So much so that the Chief surveying officer on the H.M.S. Acheron reported that "[the forests of] Banks Peninsula alone would supply [timber for] twenty Canterbury settlements for centuries" (Letter dated May 8 1849, cited in Petrie 1963) The change from a forested landscape to one which is now essentially grassland was achieved through the activity of the early settlers in the 19th century. The forests were used as a source of timber to build and fuel growing Christchurch (Petrie 1963, Ogilvie 1978) and were cleared to provide agricultural land to feed a growing nation. Cocksfoot (*Dactylis glomerata*) was an important crop species on the Peninsula, and cocksfoot seed was highly sought after as the basis for establishing pasture in the young nations burgeoning agricultural sector (Petrie 1963). The cocksfoot seed industry largely died out with the cessation of large scale forest clearance in the early decades of the 20th Century.

Extensive agriculture was encouraged on the Peninsula, to the point where less than 20% of the original forest cover now remains (Petrie 1963). Now, there are a few tiny remnant patches of vegetation on the western Port Hills, existing in a condition approaching that which would have been present at the time of first European settlement. One such remnant is Ahuriri Summit Bush, a few kilometres to the south of Hoon Hay valley. There the forest consists of an irregular but almost continuous canopy of angiosperm trees, at a height of around 6-14 m. The most common canopy species are kotukutuku (*Fuchsia excorticata*), *Griselinea littoralis*, *Hoheria augustifolia*, mahoe, *Pittosporum eugenoides*, and *Pseudopanax arboreus*. Occasional emergent podocarps (mainly matai (*Prumnopitys taxifolia*), and occasional Hall's totara (*Podocarpus hallii*) and kahikatea (*Dacrycarpus dacrydioides*)), up to a height of 25 m are scattered throughout the reserve (Burrows 1994b). With the exception of kahikatea, all of these species are found in Hoon Hay valley (Wilson 1993, also Appendix 1), and although the forest has been modified to some extent it represents a working model for the kind of forest which would have been present at the time of European settlement.

6. CURRENT VEGETATION

The present day vegetation of the valley is reflective of the history of land use in the area. At the time of the first European settlement of the area the valley still had a relatively extensive coverage of mixed podocarp/angiosperm forest, and in the 1850's the valley was "filled with splendid bush, totara up to three metres in girth, white pine, black pine and plenty of giant broadleaf, manuka, and konini" (Ogilvie 1978). The valley was one of the first round the Port Hills to be occupied by European settlers, and it was an important source of timber for building and fuelwood and stone during the early years of Christchurch settlement. An extensive fire in 1868 destroyed most of the forest that remained. (Ogilvie 1978)

The Valley has been farmed to varying degrees for most of the time since then, and it is unlikely that any timber extraction has been done since the 1868 fire. There is a good air-photo record covering the entire valley since the start of aerial photography in Canterbury in the 1940's, and it is possible to trace the history of land use in the valley from these. Grazing has become increasingly uneconomic on the Port Hills, and it is evident from the air-photos that extensive farming has been in decline in the valley for much of the latter part of this century. The costs of scrub clearance and pasture improvement have become prohibitive and it is evident from the air-photos that no scrub clearance has been undertaken in the valley since the early 1980's. As a result the vegetation in the valley has begun to regenerate back to something approaching a pre-

European state, and now in places the valley is blanketed with a well advanced mantle of second-growth forest. Both Meurk (1994) and Wilson (1993b) attest that the vegetation present in the valley represents one of the most significant patches of continuous regenerating cover on the Port Hills.

The present vegetation is a complex mosaic of different stages of succession, from bare pasture to areas dominated by well advanced successional vegetation. Meurk (1994) identified 11 blocks in the valley with some geographical and ecological integrity, including all the areas currently in agricultural production, and this study is confined largely to three of them; class R, semi-continuous indigenous forest, class L identified as regenerating indigenous and deciduous exotic small trees over a canopy of broom, and class H, predominantly a secondary growth of indigenous bracken fern and groves of native trees, with patches of gorse, grass, and broom. Other classes were not included in this study for the reasons of practicality and accessibility. It was also known that parts of the valley were to be sprayed with herbicide to facilitate the establishment of pine plantation, so cover classes which were likely to be included in this operation were excluded.

The areas included in the study are thus a dynamic mosaic of vegetation at differing successional stages, ranging from open sites dominated by adventive grasses, through early successional vegetation dominated by bracken and introduced shrub species, more advanced regeneration with elder. Introduced plant and animal species are common, and species introductions are likely to continue as plants escape from domestic cultivation (Esler 1987a, 1987b, 1988. Esler and Astridge 1987).A more detailed description is provided in Chapter 3.

Meurk (1993) provides an estimate of the vegetation types which are likely to have been present in the valley prior to human settlement. The drier presumably north facing side-slopes would have supported a mixed podocarp angiosperm forest dominated by *Prumnopitys ferruginea* (matai) and *Podocarpus totara* (totara), emergent above *Myoporum laetum* (ngaio), *Dodonea viscosa* (akeake), *Hoheria* spp, *Alectryon excelsus* (titoki), *Psuedopanax arboreus* (five-finger), *Grisilinea littoralis* (broadleaf), *Pittosporum eugenoides* (lemonwood), *Sophora microphylla* (kowhai), *Melicytus ramiflorus* (mahoe), *Fuchsia excorticata*, *Streblus heterophyllus*, *Pennantia corymbosa* (kaikomako), *Eleaocarpus dentatus* (hinau), and *Psuedopanax crassifolius* (lancewood). On slopes with more reliable moisture - presumably those facing south- Meurk (1993) suggests that *Podocarpus hallii* would be more common, as would angiosperms requiring more reliable moisture or tolerant of poorer soils. Grassland and hardy shrub species would have been common on rocky outcrops and unstable sites.

There are several plant species of botanical and conservation interest present in the valley. Several species, notably *Alectryon excelsus*, *Dodonea viscosa*, and the native passion vine *Passiflora tetrandra* are at or near their southern natural limits in the Valley, and several others are of restricted distribution on the Port Hills and Banks Peninsula: *Aristotelia serrata*, *Carmichaelia* 'common', *Coprosma propinqua* and *C. rhamnoides*, *Lophomyrtus obcordata*, *Helichrysum aggregatum*, *Myrsine divaricata*, *Schlefflera digitata*, and *Psuedopanax arboreus*. *D. viscosa* and *Hoheria* spp. are apparently found nowhere else naturally in Christchurch, and matai is found in only two other places (Meurk 1993, Wilson 1993b).

Sheep (*Ovis aries*) have been present in the valley continuously throughout its recent history, as have possums (*Trichosurus vulpecula*) and rats (*Rattus rattus*). The movement of sheep throughout the valley has been common, although during the course of this study virtually all the sheep were mustered from the valley, and it the intention of the landowner to remove all sheep permanently from the regenerating areas (H. Graham, pers. comm.). At various times feral goats (*Capra hircus*) and pigs (*Sus scrofa*) have been present, and deer (*Cervus elaphus*) are commonly resident (John Sheridan, Valley resident, pers. comm.). Stoats (*Mustela ermina*) have been observed, as have hares (*Lepus europaeus*), although it is not known how common these are. Rabbits are present also but are apparently confined to pasture and grassland areas, and there is apparently a resident population of feral cats. There is a diverse avifauna (with a full list in Appendix 2), and although naturalised species are abundant it is reassuring to witness large and apparently healthy populations of fantails and bellbirds so close to Christchurch. Kereru were observed on a couple of occasions during fieldwork for this study, and are apparently only seasonal visitors to the valley.

CHAPTER 3

VEGETATION DESCRIPTION

1. INTRODUCTION

As described in Chapter 2, the vegetation cover of Hoon Hay Valley is a patchy mosaic of successional vegetation, with patches reflecting their history of disturbance, clearance for agriculture, and pressure of stock browsing. Vegetation pattern is complex, and even though relatively discrete patches can be delineated, they often have a high degree of internal compositional and structural heterogeneity.

A survey of the vegetation present in the Valley was carried out in order to provide a quantitative assessment of vegetation composition as a basis for structuring the sampling of seed rain and seedling recruitment, and to provide the first link in the vegetation→ seed rain→seedling recruitment successional continuum.

2. METHOD

The vegetation was stratified initially on the basis of aerial photo interpretation and an initial reconnaissance survey. Patches of relatively homogenous vegetation cover were identified on the basis of their appearance in the photos, using factors such as apparent uniformity of texture and, for the most recent photos, colour. These patches than were verified by an initial ground survey conducted in early December 1995.

On the basis of this preliminary investigation several broad vegetation types were identified ranging from bare pasture, tussock/cocksfoot grassland, patchy broom and gorse, broom/elder scrubland, through to relatively intact mahoe dominated forest. In order to focus the overall study, two distinct vegetation types were selected within which vegetation patterns could be readily identified. The first toward the top end of the Valley and dominated by scrubby species (bracken, broom, elder, *Muehlenbeckia* etc.), and the further down the Valley, containing a more continuous forest canopy dominated by mahoe. On the basis of the initial field survey these were further divided to give a total of four delineated vegetation types, each of an approximately equal area and thought to represent a different successional age. The scrub at the top of the Valley was divided into one early successional habitat type dominated by broom scrub, and another (presumably more mature) habitat type with mahoe and elder common. The forest was split in two

and one habitat type with a virtually exclusive mahoe canopy identified, and another with a more diverse canopy of mahoe and other angiosperms (*Hoheria, Pittosporum, Dodonea* etc.), thought to be the most mature vegetation cover present in the Valley. A large patch of broom-dominated scrub covering the southern flank of the Valley was excluded from the study as much of this was to be cleared to enable establishment of a forestry plantation.

Within each of these four habitat types 20 survey locations were located using a semi-random stratified technique, giving a total of 80 survey points. Compass-bearing transects were struck from the access tracks so that all the habitat types were evenly sampled. A starting point was randomly located on each transect and every 30 m from this a survey point was randomly located within a 5 m radius of the transect point (Figure 2.1). These survey points formed the basis of all further sampling.

The method of vegetation sampling used was essentially a modification of that described by Allen and McLennan (1983), and is very similar to that used by Owen (1993) and Reay (1996). Using the survey point as a centre a 5 m radius circular unbounded plot was created. The relative abundance of all species present in the survey circle was estimated for each of 3 height tiers (defined in Table 3.2 below) as the proportion of the 5 m radius unbounded circular plot covered by a downward vertical projection of its foliage. Estimates were in the form of an abundance score (Table 3.1), derived from those of Allen and McLennan (1983; which in turn are a modification of those of Braun Blanquet (1965)). Separate estimates were made for each species present in the plot in each height tier, with the result that an individual could be counted in more than one tier. No discrimination was made between individuals of different growth form, and all species were treated equally. Ferns and herbaceous ground-dwelling plants (grasses and herbaceous angiosperms) were combined into aggregate classes ('ferns' and 'herbs').

Table 3.1. Relative abundance cover classes used in the vegetation survey. After Allen and McLennan (1983).

Percent Cover	Cover Class
<1	1
1 -5	2
6 - 10	3
11-25	4
26 - 50	5
50 - 75	6
76 - 100	7

As these abundance scores represent an estimate of the 2 dimensional spread of each species, they tend to underestimate species with a significant vertical spread, and those which occur in deeper/taller height tiers. To overcome this the abundance scores were weighted (*sensu* Park 1963) by the log of the tier height interval in which they were observed, to give the corrections listed in Table 3.2. To create a tier height weight for the 'Canopy' tier, an arbitrary tier height of 7 m was taken.

Table 3.2. Vegetation tiers with tier-height corrections.

Tier	Height (m)	Correction
'Ground'	< 0.3	0.26
'Shrub'	0.3 - 2	0.99
'Canopy'	> 2	1.94

The abundance score for each species in each tier were then summed to give one vegetation score which provides an estimate of the biomass of each species at each of the 80 survey points.

In order to provide the basis for a systematic evaluation of data derived in the following assessments of seed rain and seedling recruitment, the survey plots were allocated to discrete habitat types based on the similarity of their floristic composition. This was achieved via the use of two ordination techniques; Detrended Correspondence Analysis (DCA) using CANOCO (CANOnical COrrespondence Analysis, (ter Braak 1988)), and TWINSPAN (Two Way INdicator SPecies ANalysis (Belbin 1995, Hill *et al.* 1975).

A. Ordination techniques

Ordination is the collective term for multivariate techniques that order individuals along axes on the basis of described attribute data (ter Braak 1987). The arrangement of ordered individuals along the derived axes can the be used to describe an ordination space with an X-Y scatter plot. The result of an ordination plotted with sites ordered along two axes is a two dimensional ordination space, with the first dimension provided by the arrangement of sites on the first ordination axis, and the second provided by their position on the second ordination axis. Multidimensional analyses are possible, but analysis beyond three dimensions becomes complicated and confusing (ter Braak 1987). The similarity of individuals (in this case species composition of each vegetation survey site) is reflected in their proximity in the derived ordination space - sites with similar

floristic composition are closer together in ordination space, and sites that are floristically dissimilar are further apart.

Ordination techniques can be simplistically divided into two types; direct ordinations, where information about species distribution is augmented by direct consideration of environmental variables, and indirect, where only floristic data is used in the analysis (ter Braak 1987, Whittaker 1978). When analysing vegetation data in community level investigations it is often the manner in which species composition changes across a landscape that is the object of investigation. Intuitively this pattern varies in response to environmental gradients associated with resource availability (light, nutrients, space, etc.) and other factors necessary for plant growth (substrate stability, for example). If one is particularly interested in the response of species composition to a particular environmental gradient then direct ordination techniques are particularly useful (ter Braak 1987). Direct ordinations order plots based on their floristic composition, with the additional constraint that their ordering is dependant on the environmental variables which have been investigated.

However a problem arises where the factors which have most strongly influenced vegetation pattern are not those used in the analysis, in which case direct methods have limited efficacy. There are many possible environmental variables, and even more techniques for measuring them and so it is generally difficult to be say with any certainty which factors are those controlling vegetation response. An analysis based solely on species composition, particularly in the initial stage of an investigation, is therefore likely to be more informative than one based on assumed environmental response. One can of course make *a priori* assumptions about the environmental variables to which species composition are responding, but unless a wide range of variables are investigated or the *a priori* assumptions are particularly valid, causal relationships of any predictive power are less likely to be described (ter Braak 1987, Whittaker and Gauch 1978).

As described in Chapter 2 the vegetation pattern in Hoon Hay Valley is complex, related to a variety of potentially inter-related historic environmental factors (e.g. land use history, presence/absence of browsing stock, successional stage, environmental gradients etc.). As such the environmental variables which are most likely to be controlling vegetation pattern are difficult to enumerate with any certainty or effectiveness, and are also likely to be strongly inter-dependent. For example stock behaviour may be related to aspect and altitude, and may also to responding to already established vegetation patterns. Direct ordination techniques are therefore likely to be of little use in describing the vegetation pattern in the Valley, and so indirect ordination, based solely on floristic composition, will be of greater use in analysing the vegetation pattern (Whittaker and Gauch 1978).

i. Detrended Correspondence Analysis

Detrended Correspondence analysis (DCA) is an indirect ordination technique where vegetation pattern is described using only floristic data. Correspondence Analysis (CA) is a technique of reciprocal averaging (see Hill (1973) for a description) in which two faults have been identified resulting from the mathematics involved in the analysis technique (Hill and Gauch 1980). The first is the 'arch effect' which arises because the second CA ordination axis is constrained by the analysis to be uncorrelated with the first axis, but is not constrained to be independent of it. This produces an artificial arch-shape in the ordination space which is in no way related to any pattern in the 'real world' data. In addition to the arch effect CA has the tendency to distort the relative distances between plots arranged in ordination space, such that plots that are equally dissimilar in terms of their floristic composition may be separated by unequal distances in ordination space (Hill and Gauch 1980).

Detrended Correspondence Analysis has been developed in an attempt to eliminate these faults (Hill and Gauch 1980). The arch effect is eliminated by dividing the first DCA axis into segments and subtracting a local mean value from each of the scores, such that at any point along the first axis the mean value of subsequent axes is approximately zero (Hill and Gauch 1980). The distance distortion problem is overcome by summarising the species composition of samples in each of the derived axis segments and arranging that equal differences in species composition correspond to equal distances along the axis. A result is that axes are scaled in what may be thought of as units of standard deviation (sd). A species may be expected to appear, rise to its mode, and disappear again in about 4sd, and a full turnover in species composition should occur over a similar gradient length. The exact techniques of DCA are too complicated for inclusion here, and a full account is provided by Hill and Gauch (1980).

ii TWINSPAN- Two Way INdicator SPecies ANalysis

TWINSPAN is a ploythetic divisive technique (*sensu* Hill *et al.* 1975), so called because it takes all the samples (in this case individual vegetation descriptions from each of the survey points) and divides them into groups based on the available attribute information. Earlier divisive techniques (e.g. association analysis, monothetic divisive analysis) worked on only presence/absence data and so were unable to be used to analyse abundance data. TWINSPAN overcomes this presence/absence limitation via the creation of psuedospecies whereby the quantitative abundance measure used is partitioned into a qualitative equivalent. For example in this instance, where relative

abundance scores are being used, the abundance score for an individual species can be partitioned into five psuedospecies, viz.:

mahoe psuedospecies 1 contains abundance scores up to 2
mahoe psuedospecies 2 contains abundance scores up to 5
mahoe psuedospecies 3 contains abundance scores up to 10
mahoe psuedospecies 4 contains abundance scores up to 50
mahoe psuedospecies 5 contains abundance scores greater than 50

These psuedospecies classes are non-exclusive and cumulative - if mahoe has an abundance score of 1 in a plot psuedospecies 1 would be recorded, but if mahoe had an abundance score of 150 then all 5 psuedospecies would be recorded. The resultant presence/absence species scores for each plot are then used as the basis for a reciprocal averaging/correspondence analysis ordination, the first axis of which is used to divide the plots in two about the mean of their scores. When these two groups are compared, psuedospecies which occur preferentially on one or other sides of the division are used as indicator species. Each group is then further divided about their ordination score mean, and this process is repeated as required (see Hill *et al.*. (1975) for a more detailed account of the principles of the technique).Perhaps the simplest explanation is that TWINSPAN is a technique for partitioning ordination space, and identifying sites which can be grouped together based on their floristic composition.

3. RESULTS

The floristic data obtained in the survey as described above were analysed using DCA in the program CANOCO (ter Braak 1988) using the default options given, with the exception that rare species were weighted downwards to reduce the effect of outliers on the overall result. The ordination space created by the first two DCA ordination axes is defined in Figure 3.1. Figure 3.1 presents a typically diffuse scatter of plots in ordination space. On a general level it is easily interpretable; one can readily see that as plots M2 and C7 are widely separated in ordination space their floristic compositions are obviously different. In contrast plots E1 and B5 are quite close together, so it is apparent that their floristic compositions are quite similar, and indeed there are plots whose compositions must be considered identical as they occupy the same points in ordination space. These first two DCA axes are explaining 21 % of the variation in the dataset, and the first axis has a gradient length of greater than 4sd, indicating that a complete turnover in species composition has occurred along its length (Table 3.3)

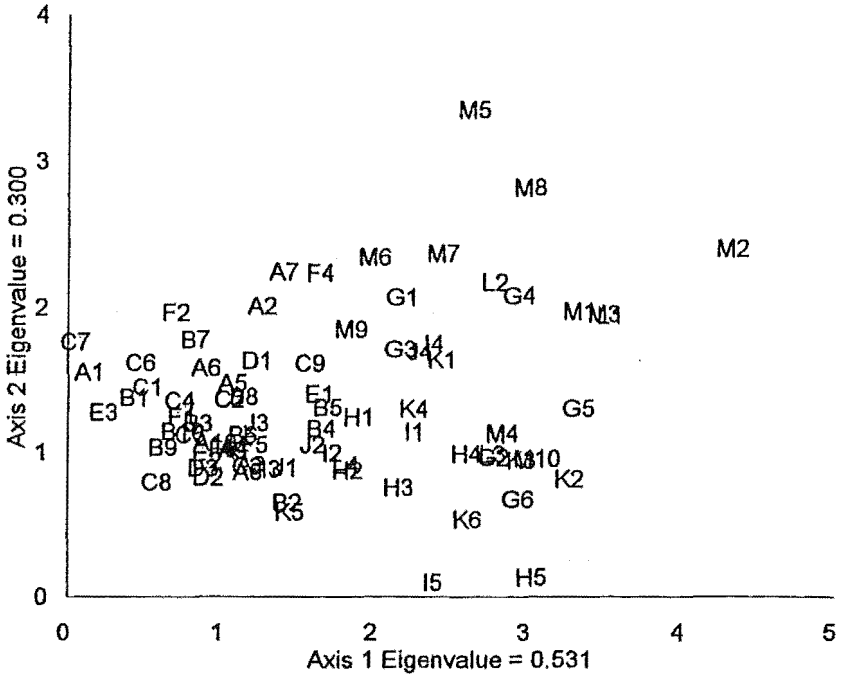

Figure 3.1. Scatter plot of DCA ordination site scores. Vegetation data. Letters correspond to transects in Figure 2.1

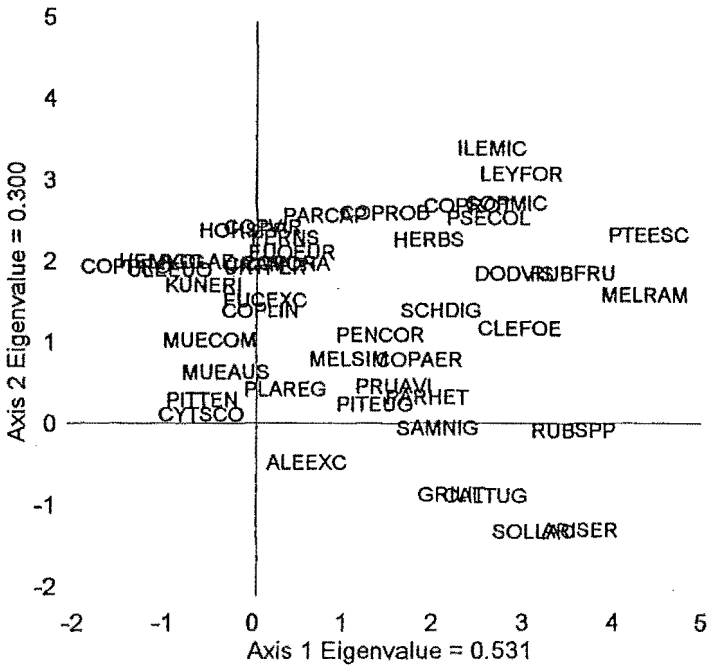

Figure 3.2 Scatter plot of DCA ordination scores. Vegetation data

Table 3.3 Summary of DCA ordination of vegetation data.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.521	0.300	0.242	0.160
Gradient length	4.279	3.256	3.012	1.773
Cum. % var.	13.4	21.0	27.1	31.1

The individual species scores derived from the DCA ordination are plotted as Figure 3.2, and analysis of these indicates which species are important in describing the vegetation pattern to which the ordination is responding. The axes of the species ordination correspond to the relative axes of the plot/site ordination (Figure 3.1). As with Figure 3.1 the trend is reasonably easy to interpret on a general level, with Axis 1 defined with mahoe and bracken at one end and an amalgam of apparently closely associated species at the other, including *Coprosma propinqua*, *Helichyrsum aggregatum*, gorse, and ngaio. The second axis is defined by *Ileostylus micranthus* and *Leycesteria formosa* at one end, and *Solanum laciniatum* and *Aristotelia serrata* at the other.

Comparison of these axis gradients with field observations indicated that the species which are apparently driving the DCA ordination described in Figure 3.1 are of only secondary importance in the Valley vegetation. To further investigate the species responsible for the overall vegetation pattern coefficients of correlation between the individual species scores and the DCA ordination scores for each of the 80 sites were defined, and these are presented in Table 3.4.

The coefficients of correlation listed in Table 3.4 indicate that the first axis is defined by forest species at one end (mahoe, ngaio, ferns. etc.) and species typical of scrubby vegetation at the other, particularly broom, bracken, and *Muehlenbeckia australis*. This corresponds much more closely to field observations and indicates that even though rare species were down-weighted in the original DCA ordination secondary species are playing a significant part in defining the ordination space described in Figure 3.1.

One of the aims of this vegetation analysis is to group plots into identifiable and floristically similar habitat types, which will provide a basis for subsequent analysis of the conceptual recruitment pathway defined in Chapter 1. As described above, the arrangement of plots in ordination space is determined by their floristic similarity. On the basis of this it should be possible to delineate habitat types based on the proximity of plots in ordination space. Where plots in ordination space are reasonably clearly clumped delineation of groups is relatively easy. However, where points are diffusely arranged, or arranged with no immediate pattern as in Figure 3.1, this grouping is difficult and relies on a significantly subjective interpretation.

Table 3.4. Pearson product moment correlation coefficients (*r*) for DCA ordination scores with species abundance scores at each of the 80 vegetation survey locations. Only species with $|r| > 0.25$ tabled.

AXIS 1		AXIS 2	
SPECIES	DCA SCORE	SPECIES	DCA SCORE
MELRAM	-0.49	MELRAM	-0.39
MYOLAE	-0.47	ARISER	-0.34
FERNSPP	-0.45	FUCEXC	-0.33
PITTEN	-0.33	RBUSPP	-0.32
URTFER	-0.27	SCHDIG	-0.26
PITEUG	-0.26	CYTSCO	0.25
SOPMIC	-0.26	PTEESC	0.25
HELAGG	-0.26	GRILIT	0.28
CRAMON	-0.25	HOHSPP	0.37
MUEAUS	0.43		
PTEESC	0.54		
CYTSCO	0.59		

As a first step to delineate habitat types for the Hoon Hay Valley data, the 80 plots were bounded based on the four subjectively defined habitat types described in the Method above (Figure 3.3).

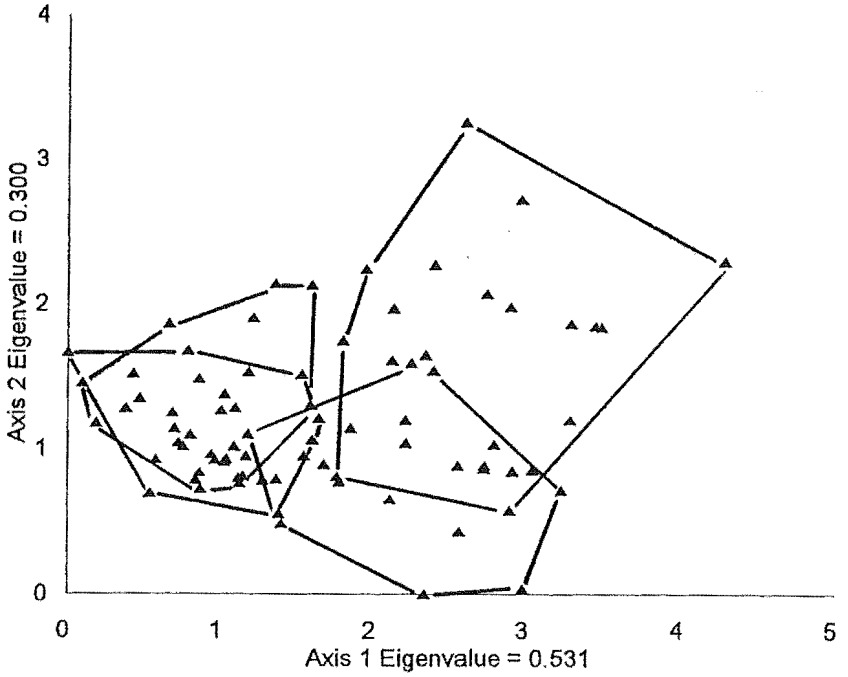

FIGURE 3.3 Figure 3.1, with first subjectively defined habitat types

These four habitat types offer an apparently good separation of ordination space, and there is some justification for accepting them as valid on the basis of this. However the factors used to subjectively define them may not be related to floristic composition. As described above habitat types were defined based on their appearance in aerial photographs. Even though the photograph interpretation was verified by an initial ground survey this was not done on a rigorously quantitative or subjective basis. It is possible that the separation groups delineated in Figure 3.3 may be due to factors other than floristic composition such as environmental gradients (altitude, aspect, etc.) or successional stage. As the aim of this stage of the analysis is to identify habitat types based solely on floristic similarity an objective technique for identifying floristically similar sites is required.

As discussed above, TWINSPAN offers a technique for the objective partitioning of ordination space. The vegetation dataset was analysed using the TWINSPAN capabilities of the PATN analysis package (Belbin 1995). The first division produced two approximately equal sized groups of plots and each of these was then further divided to give four groups of rather unequal size; two 'forest' habitat types (F1 = 28 plots, F2 = 10 plots) and two 'scrub' habitat types (S1 = 15 plots, S2 = 27 plots). These groups were used to divide the ordination space described in Figure 3A into four habitat types These are plotted as Figure 3.4

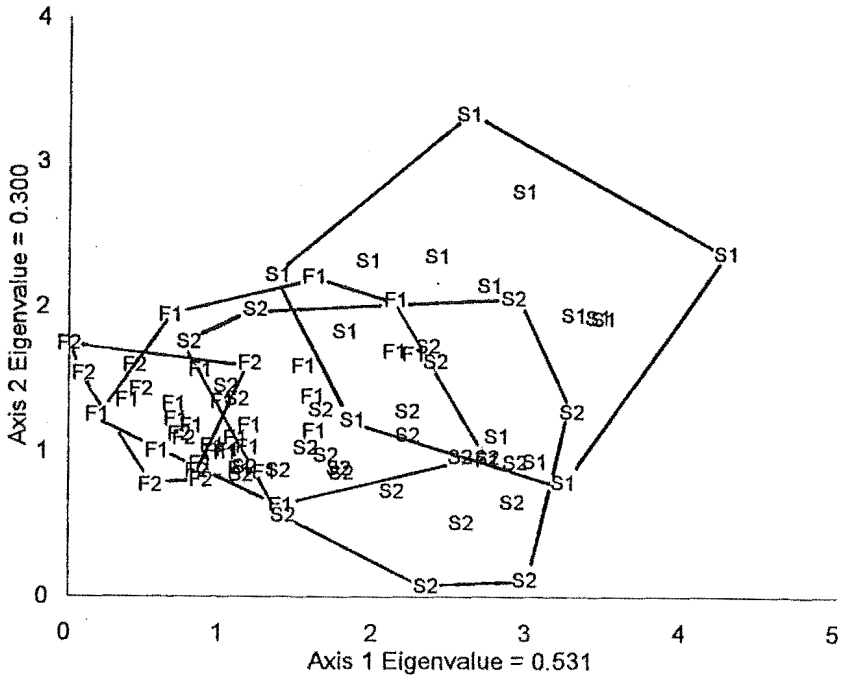

FIGURE 3.4 Figure 3.1 delineated with TWINSPAN derived habitat types

On first impressions Figure 3.4 is a less satisfactory delineation than that of Figure 3.3. The 4 groups are of unequal size, and contain significantly different variation in their floristic composition. For example group S1 contains about half the number of plots (15) than are in S2 (27), but occupies virtually the same quantity of ordination space. They are significantly more variable than those in S2, but sufficiently different to be divided by the TWINSPAN output. Groups F1 and F2 occupy ordination space consistent with their relative sizes, indicating that they contain a similar amount of floristic variation. But as can be seen in Figure 3.4 there is a significant amount of overlap in their occupancy of ordination space. Delineation based on objective TWINSPAN output offers a substantial improvement over the subjective delineation of Figure 3.3, and these four delineated groups have been used as the basis for all subsequent analysis.

The four habitat types derived from the TWINSPAN analysis above were then described using the naming system of Aktinson (1985). This is a descriptive naming system, with derived names conveying information about species composition, species diversity, and structural complexity in a systematic and repeatable fashion, allowing a more precise nomenclature than would be possible with a more simple naming system.

To adequately describe and name the habitat types, species abundance data was combined for each of the four habitat types, and then weighted for the number of plots in each habitat type. These weighted species abundance scores ranged from <<1, to greater than 100, and in order to simplify the classification process only those species with weighted abundance score greater than 1 were used (Table 3.5)

In the naming system of Atkinson (1985), underlines indicate a dominant component, plain text indicates a major component, and parentheses indicate a minor but significant component of each vegetation structural tier. Species separated by a hyphen make an equal contribution, and a '/' separates structural tiers. Forest is defined as "woody vegetation in which the cover of trees and shrubs in the canopy is greater than 80% and in which the tree cover exceeds that of shrubs. Trees are defined as woody plants with stem diameter greater than 10 cm", and Scrub is defined as "woody vegetation in which the cover of shrubs and trees in the canopy exceeds 80 % and in which shrub cover is greater exceeds that of trees. Shrubs are woody plants with stem diameter less than 10 cm."

Table 3.5. Weighted abundance score for all species with score greater than 1 for each of the four TWINSPAN-derived habitat types. Species codes are defined in Appendix 3.

F1		F2		S1		S2	
Species	Score	Species	Score	Species	Score	Species	Score
MELRAM	115.6	MELRAM	17.7	CYTSCO	25.8	MELRAM	68.5
MYOLAE	20.5	MYOLAE	14.5	HOHSPP	23.2	SAMNIG	48.5
KUNERI	19.3	PITTEN	14.0	MUEAUS	8.2	MUEAUS	13.1
SAMNIG	16.7	DODVIS	8.0	SAMNIG	6.8	CYTSCO	10.8
HOHSPP	16.0	SOPMIC	7.5	ARISER	6.2	HERSPP	8.6
PITEUG	15.7	HERSPP	4.5	HERSPP	6.0	PITTEN	4.6
COPROT	7.8	COPCRA	2.8	PTEESC	2.5	ARISER	4.5
HERSPP	6.0	PRUAVI	2.7	MELRAM	2.0	SCHDIG	4.5
SOPMIC	2.9	COPVIR	2.4	COPVIR	1.4	CALTUG	2.4
MUEAUS	2.4	HELAGG	1.7			PARHET	2.3
PARHET	1.3	COPLIN	1.3			EUOEUR	1.4
PENCOR	1.2	PITEUG	1.3			KUNERI	1.3
		MELSIM	1.1			RUBFRU	1.2

On the basis of the information presented in Table 3.5 and with supplementary observations taken during the initial ground survey, the following habitat type names were derived.

- F1 = Mahoe(Ngaio)/*Coprosma* spp.(Elder) Forest
- F2 = Mahoe(Ngaio-*Pittosporum*)/*Coprosma* spp.(Kowhai) Forest
- S1 = Broom-*Hoheria*/*Muehlenbeckia* Scrub
- S2 = Mahoe-Elder/*Muehlenbeckia*(Broom) Scrub

A description of each habitat type is given below. In order to augment the information provided by this nomenclature an array of summary statistics was compiled. Firstly the total relative biomass of each survey point was derived, and these averaged to give a mean biomass relative biomass for each of the habitat types. Secondly the species diversity of each of the habitat types was calculated, and these scores compared. Diversity is a widely used measure in ecological studies and is a valuable tool for comparing sites (Magurran 1988). Diversity as measured in ecology has two contributors, variety and the relative abundance - it takes account of the number of

species present along with a weighted measure of their relative abundance (Magurran 1988). To assess the diversity of the floristic composition of the derived habitat types the Shannon Weiner diversity index (H') was derived for each of the survey points using the following formula (from Magurran 1988):

$$H' = |\Sigma(p_i(\log_2 p_i))|$$

Where p_i = the proportion of total cover (in this case the proportion of total relative abundance) contributed by the *i*th species at each survey point. The derived diversity indices were average to give a mean diversity index for each habitat. These were significantly different at the 95% level (Table 3.6)

Table 3.6. Comparison of mean standing biomass and species diversity for each of the four TWINSPAN derived habitat types.

		F1	F2	S1	S2	F	*p*
n		28	10	15	27		
BIOMASS	**Mean**	231.04	231.05	150.53	190.35	15.76	<0.00
	s.d.	83.57	96.31	60.62	68.38		
	Duncan's[1]	A	A	B	AB		
DIVERSITY	**Mean**	1.43	1.61	1.47	1.25	7.59	<0.00
	s.d	0.72	0.63	0.39	0.52		
	Duncan's	B	A	BC	C		

[1]Habitat types with same letter are not significantly different at 95% level

A Duncan's Multiple Range test separated the scrub and forest types at the 95% level on the basis of their biomass scores (Table 3.6), indicating that the forest types had significantly greater biomass that the scrub types. In the scrub types S2 was not sufficiently different to be separated from either S1 or the two forest habitat types. Diversity exhibited significant differences between the four habitat types. The types can be ranked from F2 containing the highest diversity followed by F1. Type S1 is intermediate between F1 and the type with the lowest diversity, S2.

The structural complexity of the habitat types was not directly assessed in this study. It can however be estimated by consideration of the standard deviation of mean biomass scores for each Habitat types. Structural complexity is reflected in variability in total relative biomass, and the magnitude of the between-site structural variability for each habitat type is reflected in the magnitude of the standard deviation of the total biomass scores for each habitat type. Consideration of Table 3.6 indicates that the forest types

have greater structural complexity than the scrub types as they have larger standard deviations of mean biomass than the scrub types.

a. Characteristics of derived habitat types

i. Forest types

F1. Mahoe(Ngaio)/*Coprosma* spp.(Elder) Forest

28 sites were allocated to Habitat Type F1. The canopy of habitat type F1 is dominated by mahoe, with a weighted abundance score of 115.6. The next most abundant canopy species is Ngaio, which is more evenly distributed that either kanuka or elder. These are the next most abundant species and at a finer scale of sampling or mapping would probably be delineated as separate habitat types. *Coprosma* species, particularly *C. rotundifolia* and *C. virescens* are abundant in the understory, and elder makes a minor but significant contribution to understory biomass. The canopy is fairly uniform and low, only infrequently exceeding about 7 m in height.

F2. Mahoe(Ngaio-*Pittosporum*)/*Coprosma* spp.(Kowhai) Forest

10 sites were allocated to Habitat Type F2. Mahoe is also the most abundant canopy species in type F2, and both Ngaio and Pittosporum (particularly *P. tenuifolium*) make a significant contribution to the canopy. Akeake (*Dodonea viscosa*) is locally abundant, although apparently confined to the moister sites toward the bottom of the Valley. Kowhai (*Sophora microphylla*) makes a minor but significant contribution to both the canopy and understory, and as with F1 *Coprosma* spp. are abundant in the understory. *Coprosma linarifolia* forms a low canopy at about 5 m height at a couple of sites. The canopy of F2 is more variable than that of F1 as evidenced by comparison of the standard deviations of relative biomass scores in Table 3.6; F2 has a s.d of 96.31 compared with 83.57 for F1. Several individuals of *Ileostylus micranthus* (a native mistletoe) were observed which are apparently becoming increasingly rare on the Peninsula (Wilson 1996). All individuals observed were parasitising *Coprosma virescens*, although it is likely that other species in the Valley will be *Ileostylus* hosts (Wilson 1996).

ii. Scrub Types.

The scrub types are quite different from the Forest habitat types. They typically have lower relative biomass scores, and are on average less diverse than the forest types. They are structurally patchier than the Forest types, although this is not reflected in the standard deviation comparisons of Table 3.6, due probably to the fact that they have lower relative biomass. In both type vines are common and abundant, so much so that at times passage is exceedingly difficult.

S1. Broom-*Hoheria/Muehlenbeckia* Scrub

15 sites were allocated to Habitat Type S1. Broom is the dominant species in this habitat type, and although *Hoheria* has a very similar relative abundance score is distribution is much more patchy than for broom. Large scattered individual *Hoheria* trees are spread throughout this habitat type, and their size and apparent age indicates that they may be either remnants of previous vegetation, or have arisen quite quickly after some of the earliest vegetation clearance. Several clumps of large *Hoheria* trees are identifiable from the beginning of the aerial photo record.

S2. Mahoe-Elder/*Muehlenbeckia* Scrub

27 sites were allocated to Habitat Type S2. S2 is dominated by Mahoe and Elder in the canopy, which is somewhat patchy and only infrequently extends higher than about 5 m. *Muehlenbeckia* vines are abundant, as are both the *Parsonsia* species and the native bindweed *Calystegia tuguriorum*.

4. DISCUSSION

It is clear from the diffuse spread of plots in the ordination space of Figures 3.1 to 3.3, and from the results presented in Table 3.6 above, that the vegetation present in Hoon Hay Valley offers considerable spatial variability in terms of both species composition and structural complexity at the scale at which the vegetation was surveyed. The pattern is complex, and the without the objective TWINSPAN analysis delineation of vegetation types in ordination space presented would be just one of a number of possibilities. The comparisons offered in Table 3.6 indicate that the four habitat types are sufficiently different to provide a useful basis for investigating the conceptual recruitment continuum which forms the basis for this study.

As described in Chapter the patterns of vegetation in Hoon Hay Valley have already been investigated in some manner by Williams (1983), Wilson (1993b), and Muerk (1993). Apart from Williams (1983) these are descriptive studies designed to investigate areas of potential significance for conservation (Wilson 1993b) or to present and assess options for land use in the Valley in the case of Meurk (1993). Williams (1983) investigated processes of succession and concluded that vegetation followed a broom→elder→mahoe succession. This was broadly similar to the kanuka→mahoe succession observed by Druce (1957) in the Taita experimental catchment in the Hutt Valley, and on the basis of this Williams (1983) suggested that broom and elder had to a certain extent taken over the role of kanuka as a secondary successional species on the Port Hills. Williams (1983) observed that broom had a lifespan of around 15 years in Hoon Hay Valley (based on growth-ring counts), after which time elder tends to dominate the vegetation. Mahoe

probably establishes in the canopy within 10 years of elder establishing, and it probably takes only another 10 or 20 years for mahoe to be the dominant canopy species; a total of 50 years since the establishment of broom. Williams (1983) suggested that this broom →elder→mahoe succession fitted the facilitation model of Connell and Slatyer (1972), whereby later successional species can only grow once earlier ones have suitably modified the environment, and that non-native species were playing an important role in this process. It is interesting to note that gorse is not an important successional species in the Valley, although it is apparently important is similar environments (Lee *et al.* 1986)

With this in mind, based on the vegetation analysis presented here the habitat types can be arranged on a successional continuum from least mature to most mature. Type S1 is dominated by broom, so would logically come first on the successional pathway, followed by Type S2. It is interesting to note the presence of *Hoheria* in S1, which perhaps represent remnants from previous vegetation. S2 is dominated by the later successional species mahoe and elder, but still has a significant broom component. *Muehlenbeckia* vines are also a dominant part of both these habitat types, and the presence of this and a significant broom component indicate that S2 is toward the early end of Williams' successional continuum. The two forest habitat types are placed next on the continuum, and are a little more difficult to separate. However the presence of kanuka and elder in F1 in important quantities indicates that this type is earlier on the continuum that F2, which has a greater proportion of species which would be indicative of more mature forest.

This presumed successional pathway is confirmed by investigation of the diversity analysis presented in Table 3.6. The more mature habitat types have the greatest diversity (F2 followed by F1), which are significantly different from the less mature scrub habitat types. It is interesting to note that the presumed least mature type (S1) has diversity intermediate between the forest types and the type with the lowest diversity (S2), and that the type with the lowest diversity is not the youngest on the presumed successional pathway.

This continuum is however complicated by the presence of browsing and stock damage, and by the presence of remnant vegetation from earlier successions. The effect that stock has had on the current vegetation is rather difficult to quantify, as no detailed records have been kept of stock movements (particularly for feral animals), and save for the history of land use provided by the air-photo record of the Valley and sketchy anecdotal histories, little is definitely known about the vegetation history. In spite of all these inadequacies, the habitat types presented here are sufficiently different to be of use in the proceeding analysis, and the complex nature of the vegetation pattern apparent in the

analysis is simply an indication of the 'real world' complexity of vegetation pattern present in Hoon Hay Valley

CHAPTER 4

SEED RAIN

1. INTRODUCTION

Seed rain provides the second step on the vegetation→seed rain→seedlings conceptual recruitment continuum. The seed rain stage also represents the point at which dispersal presents the greatest opportunity for vegetation change, and so an assessment of spatial and temporal patterns of seed dispersal represents a key link in the study of successional change in Hoon Hay Valley.

Successful regeneration by a plant depends on seeds or other propagules (any unit by which plants multiply themselves (Burrows 1990)) being dispersed to site where they can germinate and grow into seedlings (Fenner 1985). As Haper says "succession depends on the fugitive properties of plants. All successional species are doomed in their present habitats, and their continued survival depends on escape and establishment elsewhere." (Harper 1977, p34). Seed rain declines exponentially with increasing distance from the parent plant (Harper 1977 and references therein, Howe and Smallwood 1982, Herrera 1984, Howe *et al* 1985 Silvertown 1987 Tilman 1988), and so there are strong selective pressures in favour of the dispersal of propagules away from a parent plant (Gadgil 1971, Willson 1993a). This is particularly true for successional species (Harper 1977), such as those which dominate the vegetation of Hoon Hay Valley.

The dispersal of propagules away from a parent can be by a variety of means depending on the species concerned and the environment they occupy. Dispersal may be by abiotic vectors, such as wind, water, gravity, or some combinations of these, or mediated by the behaviour of animal (biotic) vectors, such as insects, birds, and other vertebrates (Ridley 1930, van der Pijl 1969, Murray 1986, Fenner 1985, Howe 1986). Secondary dispersal can occur when seeds are removed from where they were first dispersed, as when insects remove and disperse seeds from frugivore defecations (Byrne and Levey 1993).

Several species of seed in Hoon Hay Valley have adapted for abiotic dispersal. Seeds of *Parsonsia* and *Clematis* are small and light and have feathery attachments which catch the wind very effectively, enabling them to be dispersed wide distances. Seeds of *Hoheria* are adapted for dispersal by a combination of wind and gravity - the seeds have a papery achene attached which acts as a wing, which as the seeds fall from the parent causes the seeds to be dispersed a short distance, rather like the 'helicopter' seeds of *Pinus* spp. Gorse and broom have ballistically dispersed seeds; seeds are contained in a

pod which, by the end of summer has ripened to a black colour and dried out considerably. On hot days one side of the pod dries more than the other, placing a torsional strain on the pod. Eventually this stress becomes too great, and the pod explodes open propelling the seeds within it several meters away from the parent.

Aside from these most of the seed producing species in the Valley have evolved to take advantage of biotic dispersal. Biotic dispersal is dispersal by animals - zoochory in the sense of van der Pijl (1969). *Exozoochory* is external biotic dispersal - seeds are attached to the outside of animals and are dispersed when they fall off or are removed by the animal. Examples from Hoon Hay Valley include *Acaena* spp. and the hook grass *Uncinnia leptostachya*. *Endozoochory* is the dispersal of seeds inside animals. Generally seeds are ingested, and are later voided either via regurgitation or, once passed through the intestinal tract, voided in the faeces. This is usually associated with frugivory, or eating of fruit (Howe 1986). Frugivory may involve seed damage, in which case the result is seed predation rather than dispersal, or seeds may be voided relatively unharmed, in which case dispersal is the result (Murray 1986, Fenner 1992).

Frugivory is an interaction between plants and the animals which eat their fruit and disperse their seed (Howe 1986). This interaction is the subject of a burgeoning literature, particularly resulting from studies in tropical systems (e.g. Fleming and Estrada 1986, Fleming and Estrada 1993). In general terms frugivory is a mutualism, as both participants derive some benefit from the relationship - the frugivore gets a food benefit via the consumption of fruit or other accessory tissue, and the plant gets its seed dispersed, thus deriving benefit from increased dispersal (Howe 1984, 1986, 1993; Tilman 1988, McNally 1995).

Monkeys and other arboreal mammals are important frugivores in the tropics (e.g. Howe 1980, 1986, Galutier-Hion *et al.* 1993), but in temperate ecosystems it is birds which are the predominant frugivorous seed dispersal vectors (Howe 1986, Willson and Whelan 1990). Virtually all studies of seed dispersal in New Zealand forests underline the importance of birds as dispersers of seed (Burrows 1994a, 1994b, 1994c, 1994d; Clout and Hay 1989, Norton 1991, Sem and Enright 1995, Clout and Tilley 1992, but see Whitaker 1987, who suggests that lizards may have been historically significant seed dispersers). Burrows (1994a) asserts that frugivorous dispersal of seed by birds is particularly important in the forests of Banks Peninsula; of 120 woody Peninsula plant species, Burrows (1994a) presents evidence that 77% are bird dispersed.

Further evidence for the importance of generalised bird dispersal in the Banks Peninsula flora is the observation that the most frequent fruit colours are purplish black or red, which are commonly cited as the most important colours for bird dispersal in temperate

floras elsewhere (Willson and Whelan 1990). Many of the fruits of Peninsula plants are of a suitable size to be dispersed by the birds present, currently and historically. Burrows (1994a) observes that 91% of fruit species are less than 8 mm in diameter which makes them ideally suited to the Peninsula bird disperser assemblage (Clout and Hay 1989), and for those fruits larger than this there would have been present historically bird species with a gape size large enough to be able to process the fruits (Atkinson and Greenwood 1989, Caughley 1989) The proportion of fleshy fruited species in the Peninsula flora differs little from that in the national flora (Burrows 1994d), which is apparently high among the temperate florae (Clifford 1993, Willson *et al.* 1989). Burrows (1994d) opines that this may be related to the tropical phylogenetic origin of many of the species.

Given the potential benefits to successional plant species of dispersal described, and that seed dispersal presents the first opportunity for spatial vegetation change, an investigation of spatial patterns of seed rain will yield considerable insights into processes of vegetation change in Hoon Hay Valley.

2. METHOD

To assess seed rain in the four habitat types an array of 80 seed traps was deployed, with a trap randomly placed within a 5 m radius of each of the survey locations previously described. Each seed trap consisted of a galvanised steel No. 8 wire ring, 50 cm in diameter. A rectangle of dense shade cloth 157.08 cm (π50 cm) long and approximately 60 cm wide was cut and stapled firmly together at the ends to give a cylinder 50 cm in diameter and ca. 60 cm deep. This was then attached to the steel ring with stainless steel staples, and firmly tied with string at the non-ring end to give a large collecting cup. The contrivance was nailed to three 25 x 25 mm tanalised wooden 1 m long stakes, which were then hammered into the ground. The mouth of the collecting cup then stood level between 60 cm and 80 cm above the ground as in Figure 4.1. Eighty traps were deployed, each with a collecting area of 0.196 m^2, giving a total collection area of 15.71 m^2 spread over the 4 habitat types.

Traps were installed in the first week of January 1996, and were emptied every two weeks until the end of April 1996 and once more four weeks after that to give a total trapping period of around five months. Previous studies had indicated that the main period of seed fall for most of the species present in Hoon Hay Valley would have finished by this time (Burrows 1994a). Traps which had been knocked over or disrupted in any obvious way were emptied but not collected, as it could not be guaranteed that they had been collecting for the whole collecting period. This occurred in only 19 of a possible 640 trap clearances, or less than 3% of the time.

Figure 4.1. One of the seed traps used in this study

To clear the traps the string tied around the bottom of the trap was removed, and a paper bag held under the opening. A large sheet of plastic was spread beneath the trap to catch any trap contents escaping either the paper bag or the trap once it was untied. All the trap contents were then pushed down through the open trap bottom into the paper bag below, and any escaped material retrieved from the plastic sheet.. The bag was then stapled shut and the string around the base of the trap firmly re-tied. The bags of trap material were then taken back to the laboratory where they were stored prior to sorting. Paper bags were used so that the trap material could dry out during storage, preventing the germination of trapped seeds and rotting of other trap contents.

After the final trap clearance in May, the 621 bags of stored material were opened, and their contents sorted. Seeds and fruit were separated from other material (leaves, twigs, frass etc.). These were identified to species, and the numbers of whole and damaged seeds and fruit counted. Seeds which were not able to be immediately identified were given a discrete number and a small sample kept separate. These were later identified by comparison with material collected in the field, herbarium material, or in consultation with others, notably C. J. Burrows, M. O'Cain, and D. A. Norton. Further unknown seeds were compared against these samples and either numbered according to the sample they matched, or similarly separated and numbered. All except four seed species were able to be identified.

It had been hoped to identify individual bird defecations and analyse the seed deposited within these, but it quickly became apparent during trap clearance that individual discrete faeces were unable to be identified and so this was not done. However a large number of discrete faecal clumps of the brush tailed possum (*Trichosorus vulpecula*) were caught in the traps and these were separated from the other trap material. The faecal clumps from each trap clearance were then broken up with careful crushing, and the whole seeds present separated and identified to species. Significant numbers of damaged seed were observed, particularly of mahoe and elder, but because of the large difficulties in extracting small particles of damaged seed from other faecal matter, damaged seeds were treated the same as other faecal material and so only whole undamaged seeds were counted. It was not possible to identify which clumps had come from discrete faecal events, so the total faecal mass for each trap was aggregated and treated as a single faecal unit.

Once sorting and counting were completed the bags of separated material were dried to a constant water content in a forced draught oven at 80° C for 48 hours. The separated seeds and other material were then weighed to the nearest 0.001 gram.

3. RESULTS

1. Seed Rain

Table 4.1 presents the results of seed trap sorting, excluding those seeds trapped in possum faecal clumps, which are discussed separately below. 95 189 whole and damaged fruit and seeds were counted from 46 predominantly woody species.

This gave on average a seed rain of 3875 whole seeds m^{-2} over the five months, and a total average of 6070 whole and damaged seeds and fruit per m^2. Eleven of the 46 species contributed at least 1% of the total whole seeds, and these 11 species combined contributed 89% of the total whole seed rain (Table 4.2). Eight of the 46 species were found in at least half the traps, and 24 species occurred in fewer than 10 traps. Two species, *Melicytus ramiflorus* and *Clematis foetida*, occurred in more than 70 of the 80 traps.

Table 4.2 Occurrence of seed species contributing more than 1% of total whole-seed rain, Hoon Hay Valley, January -May 1996.

Species	Whole seeds	% of Total	in traps
MELRAM	32649	53.73	75
CLEFOE	4539	7.47	73
MEUAUS	700	1.15	60
PARSPP	2101	3.46	60
SAMNIG	1377	2.27	59
LEYFOR	1782	2.93	56
COPVIR	2272	3.74	51
CYTSCO	3189	5.25	28
HOHSPP	1962	3.23	21
ARISER	2478	4.08	14
DODVIS	981	1.61	7
Total	**54 030**	**88.92**	

Only whole undamaged seeds are considered from here on, unless otherwise stated. While the number of whole or damaged fruit will significantly increase the total number of individual seeds deposited at each trap, it proved too complicated and time consuming to consider all the seeds present within each fruit. While the number of seeds contained within each fruit can be relatively constant for each species (see for example Powlesland 1984, Burrows 1994b) this is not always the case (e.g. Herrera 1984). The total number of seeds is thus difficult to assess, especially when considering the variability in seed numbers introduced by the presence of damaged fruit, each containing an unknown number of remaining whole or damaged seeds. In any case the trend in the majority of seed rain literature is to discuss whole undamaged seeds, irrespective of the number of fruit trapped.

Table 4.1. Whole and damaged seeds and fruit caught in 80 seed traps in Hoon Hay Valley, January to May 1996 (Species codes are defined in Appendix 3)

	SEEDS				FRUIT			
	WHOLE		DAMAGED		WHOLE		DAMAGED	
Species code	n	% of tot	n	% of tot	n	% of tot	n	% of tot
ACAANS	114	0.19	4	0.04				
ACASPP	12	0.02			1	0.00		
ALEEXC	145	0.24	2	0.02				
ANTODO	393	0.65	6	0.07				
ARISER	2478	4.08			84	0.36	5	0.54
BETSPP	68	0.11	1	0.01				
BROSPP	52	0.09	4	0.04				
CALTUG	3	0.00			26	0.11		
CARSPP	21	0.03						
CLEFOE	4539	7.47	120	1.34	2	0.01	10	1.09
COPROB	383	0.63	1	0.01	27	0.11		
COPROT	514	0.85	4	0.04	2	0.01	2	0.22
COPVIR	2272	3.74	53	0.59	43	0.18	2	0.22
CRAMON	2	0.00						
CYTSCO	3189	5.25	79	0.88				
DODVIS	981	1.61	968	10.83				
EUOEUR	6	0.01			3	0.01		
HOHSPP	1962	3.23	4572	51.14				
HYPRAD	0	0.00	1	0.01				
ILEMIC	1	0.00						
JUNSPP	7	0.01						
LEYFOR	1782	2.93						
MELRAM	32649	53.73	2838	31.74	17493	74.24	604	65.58
MELSIM	306	0.50						
MEUAUS	700	1.15	6	0.07	538	2.28	246	26.71
MEUCOM	13	0.02	1	0.01				
MYOLAE	175	0.29	2	0.02	354	1.50	3	0.33
PARSPP	2101	3.46	185	2.07				
PITEUG	56	0.09			70	0.30	1	0.11
PITTEN	252	0.41	5	0.05	5	0.02		
PLAREG	66	0.11			284	1.21		
PSUARB	2	0.00						
RUBIDA	14	0.02						
RUBSPP	18	0.03	17	0.19	3	0.01	1	
RUMSPP	129	0.21						
SAMNIG	1377	2.27	29	0.32	4549	19.30	47	5.10
SCHDIG	168	0.28			80	0.34		
SOLDUL	13	0.02						
SOPMIC	216	0.36	3	0.03				
UNCLEP	141	0.23	9	0.10				
UNK002	1	0.00						
UNK003	2	0.00						
UNK004	187	0.31	30	0.34				
UNK006	2	0.00						
URTFER	2	0.00						
VICSPP	10	0.02						
TOTAL	**60764**	**100.00**	**8940**	**100.00**	**23564**	**100.00**	**921**	**100**

Seed rain at each of the 80 traps varied significantly, with the most productive trap catching 7487 whole seeds, or 12.3% of the total seed rain (38 198 seeds m^{-2}), and the least productive catching only 94 seeds (480 seeds m^{-2}) over the five month trapping period. The 10 most productive traps contributed 52% of the total whole seeds caught (Figure 4.2). The overall mean number of seeds caught in each trap (± 1 s. d.) was 759.55 ± 1139.183 to give an overall seed density of 3875 seeds m^{-2} for the five month trapping period.

1A. Temporal distribution of seed rain.

The temporal distribution of seed rain (Figure 4.3) shows a general increasing trend over the trapping period. There is a distinct peak around day 80 (March 20), which declines to a minimum around day 100 (April 9), and seed rain then increases for the rest of the trapping period.

All the species listed in Table 4.2 have differing seed rain distributions, although they generally all have a unimodal distribution with seed rain rising to a distinct peak (Figures 4.4 to 4.13). Two of the species listed apparently did not reach their maximum seed fall during the trapping period; mahoe and *Parsonsia* spp. (Figs. 4.4 and 4.9). The implications of this are potentially significant, and are discussed in following sections.

1b. Spatial Distribution of Seed Rain

i Seed rain density

As stated above there was large variation in the seed rain experienced by the 80 seed traps. The difference in whole-seed rain between the forest (F1/F2) and scrub (S1/S2) habitat types was not significant ($F=2.72$, $p = 0.10$). However at the level of the four individual habitat types significant differences in whole-seed rain are apparent (Table 4.3).

Table 4.3. Differences in mean whole-seed rain per trap for each of the four habitat types.

	S1	S2	F1	F2	F	*p*	Sig.?
n	15	27	28	10			
MEAN	281.00	1220.93	547.43	501.60	7.22	<0.00	✓
s.d.	321.17	1684.50	680.08	316.42			
Duncan's[1]	B	A	AB	AB			

[1]Note: Habitat types with the same letter are not significantly different at the 95% level

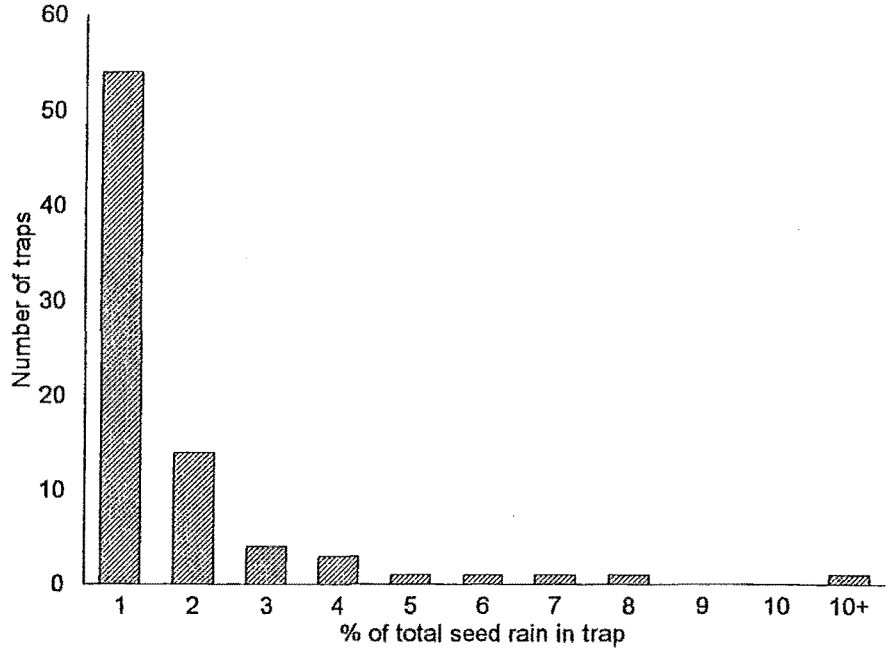

Figure 4.2. Frequency distribution: percent of total seed rain caught in the 80 seed traps

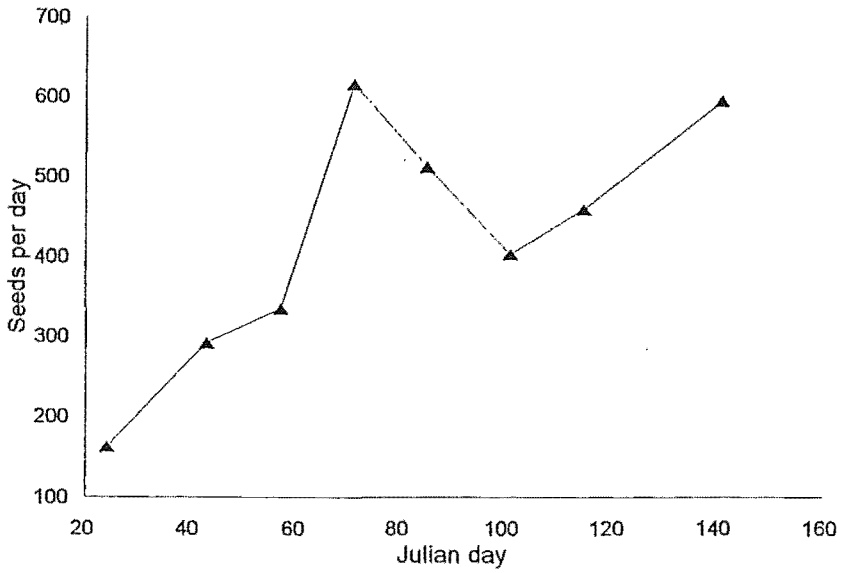

Figure 4.3. Overall temporal seed rain trend

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

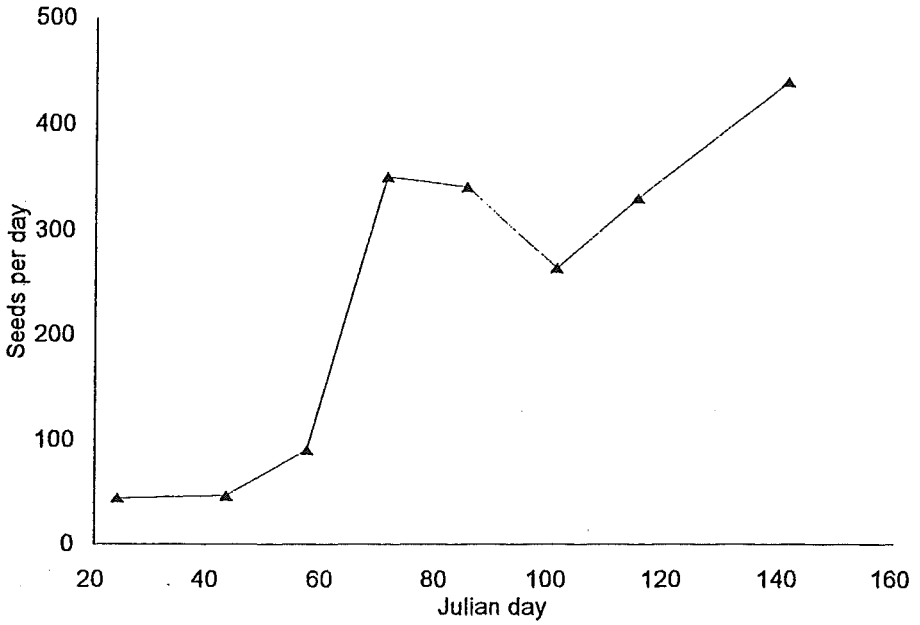

Figure 4.4. Seed rain trend: *Melicytus ramiflorus*

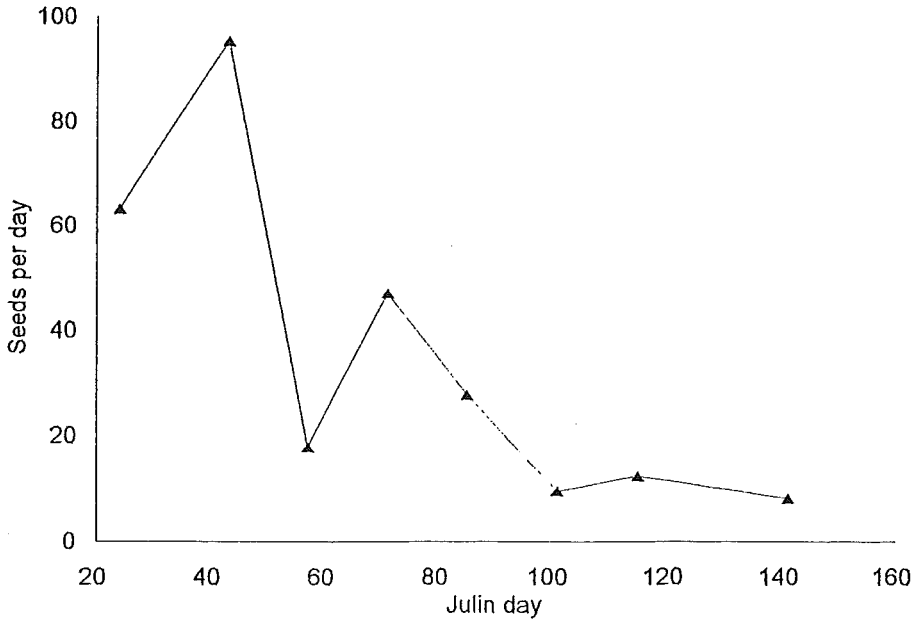

Figure 4.5. Seed rain trend: *Clematis foetida*

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

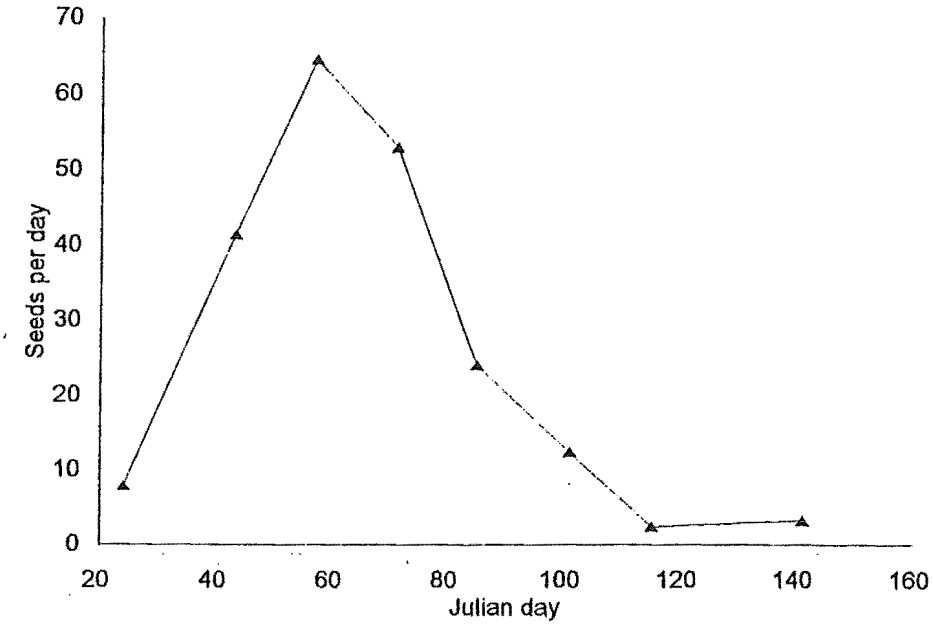

Figure 4.6. Seed rain trend: *Cytisus scoparius*

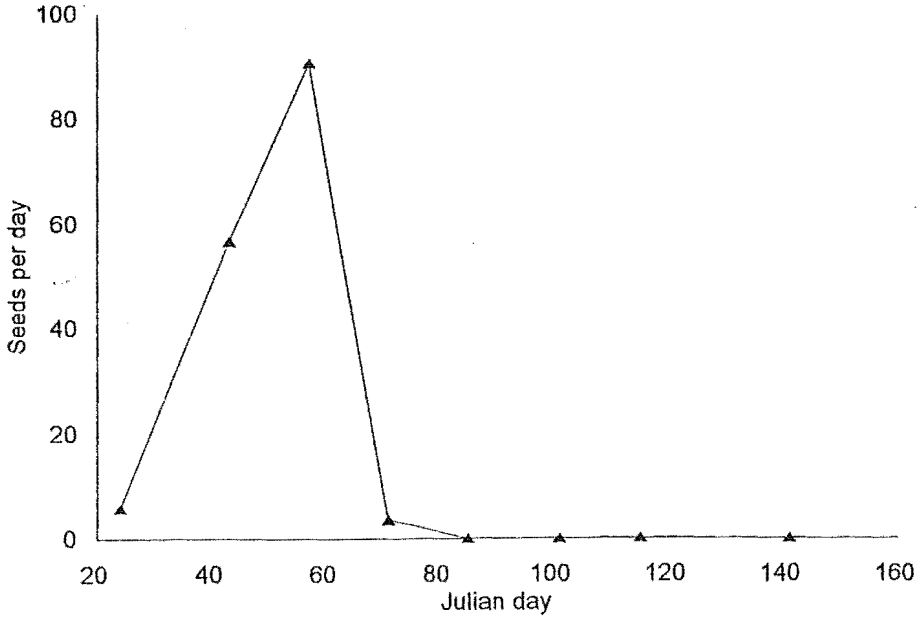

Figure 4.7. Seed rain trend: *Aristotelia serrata*

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

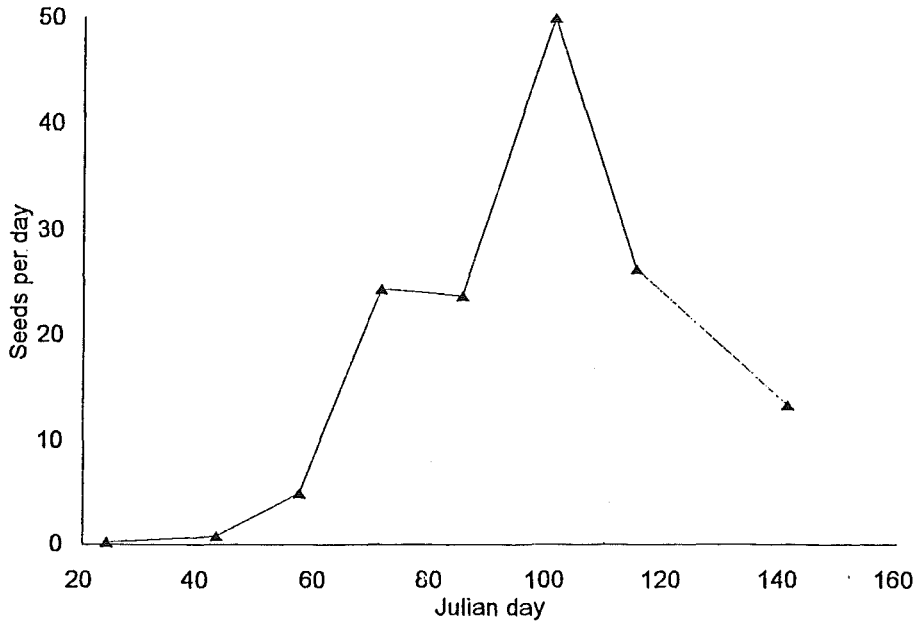

Figure 4.8. Seed rain trend: *Coprosma virescens*

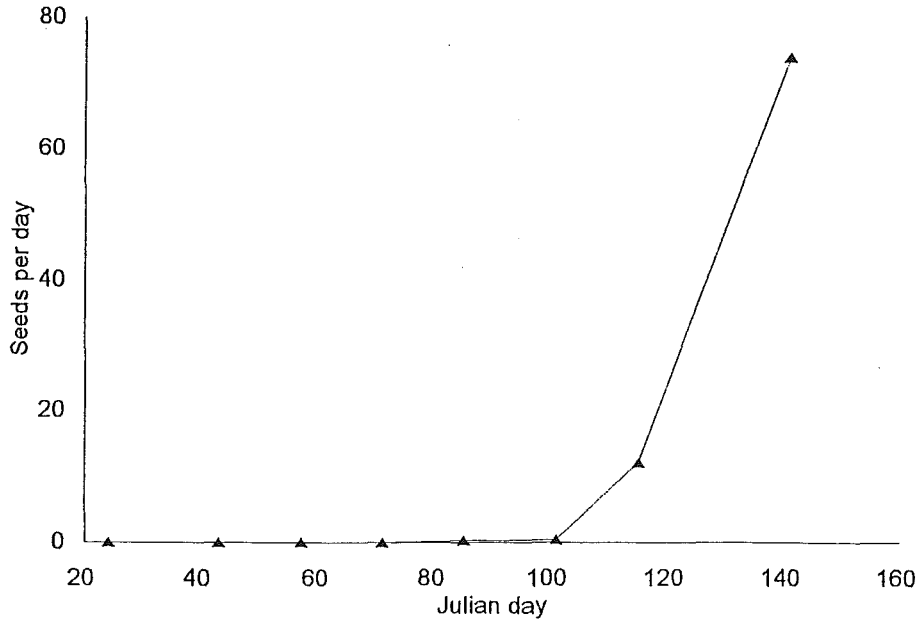

Figure 4.9. Seed rain trend: *Parsonsia* spp.

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

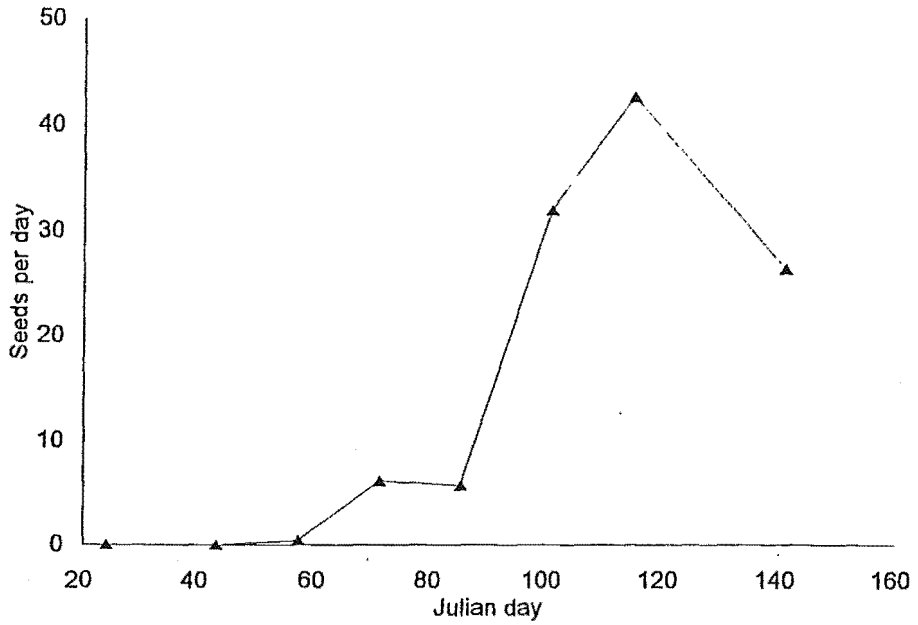

Figure 4.10 Seed rain trend: *Hoheria* spp.

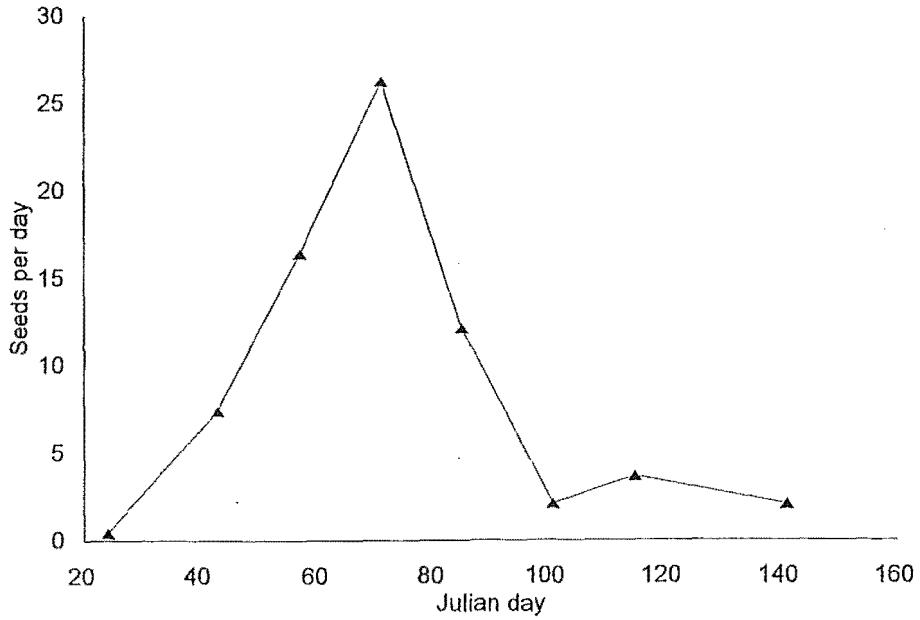

Figure 4.11. Seed rain trend: *Leycesteria formosa*

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

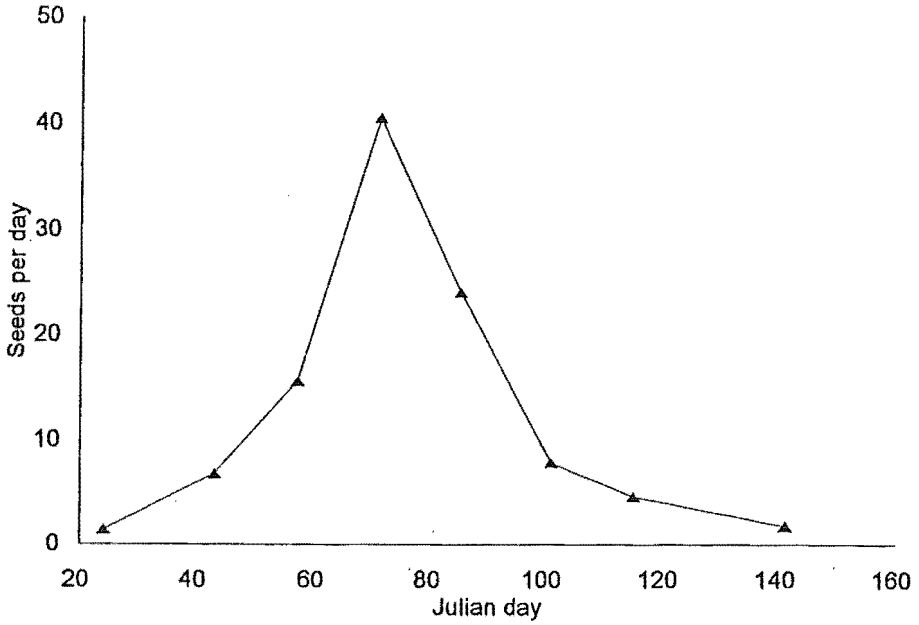

Figure 4.12 Seed rain trend: *Sambuccus nigra*

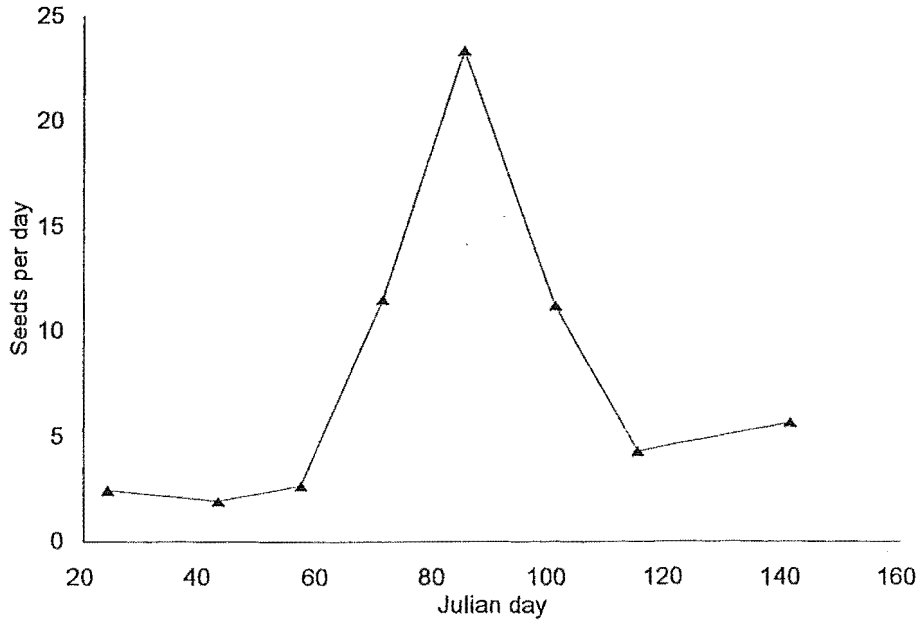

Figure 4.13 Seed rain trend: *Dodonea viscosa*

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

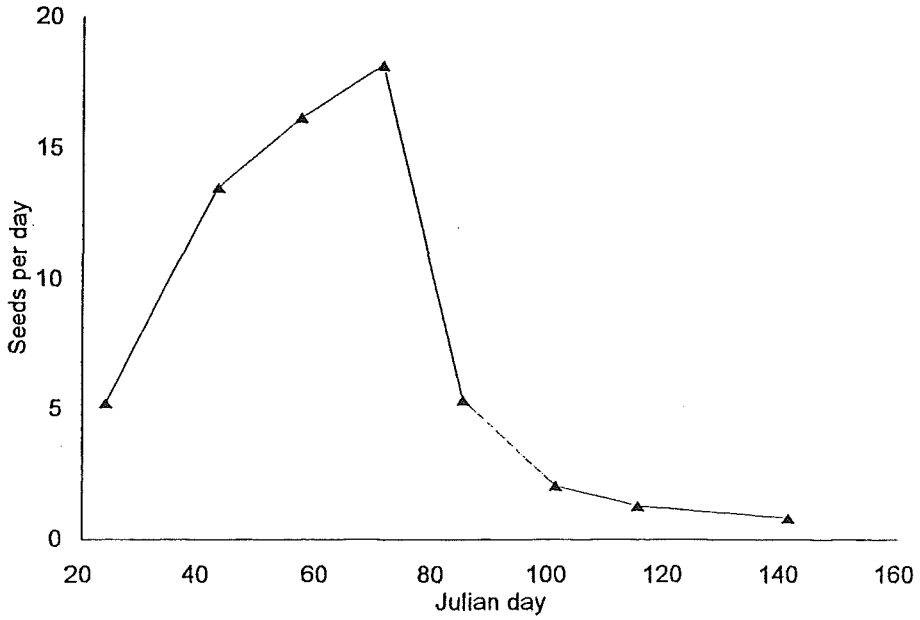

Figure 4.14 Seed rain trend: *Meuhlenbeckia australis*

Note: Julian Day 20 = Jan. 20, Day 80 = Mar. 20, Day 160 = Jun 8

Differences in whole seed rain between the four habitat types were assessed with a Duncan's Multiple Range test (Table 4.3). This separated only the two scrub types, indicating that the differences in seed rain density between them were significant at the 95% level. Whole seed rain in the forest types (F1 and F2) were not significantly different from the scrub types, or from each other (Table 4.3).

The total whole-seed rain of each of the 11 most abundant species presented in Table 4.2 exhibited large variation between the four habitat types, which was significant for all but three species, *Coprosma virescens*, *Hoheria* spp., and *Dodonea viscosa*. (Table 4.4).

Table 4.4. Differences in mean whole-seed rain (seeds m^{-2}) for each of the 11 species from Table 4.2.

Species	S1	S2	F1	F2	F	*P*	Sig.?
MELRAM	100.33	825.78	309.89	134.50	4.85	0.00	✓
CLEFOE	3.60	24.33	108.37	79.40	7.09	0.00	✓
CYTSCO	137.87	41.48	0.04	0.00	3.79	0.01	✓
ARISER	0.07	91.41	0.29	0.10	2.72	0.05	✓
COPVIR	4.20	24.33	16.64	108.60	1.19	0.32	**no**
PARSPP	1.00	55.00	17.71	10.50	5.26	0.00	✓
HOHSPP	83.87	2.78	22.46	0.00	0.88	0.45	**no**
LEYFOR	4.40	41.63	18.50	7.40	5.17	0.00	✓
SAMNIG	4.27	37.15	10.61	1.30	11.76	0.00	✓
DODVIS	0.00	0.00	0.07	96.20	2.05	0.11	**no**
MUEAUS	7.73	16.56	4.64	0.70	8.87	0.00	✓

ii. Ordination

The seed rain scores at each of the 80 seed trap sites was used as the basis for a DCA ordination and this is presented in Figure 4.15. The seed rain ordination is substantially more clumped than the vegetation ordination presented in Figure 3.1, with a significant clump of ordination points about (3,2) consisting almost entirely of plots from S1, indicating that the seed rain is highly homogeneous for this habitat type. The gradient length of the second DCA axis is longer than that of the first (Table 4.5), and while this is not immediately apparent from a plot of the site scores (Figure 4.14) it is when the individual species scores are plotted (Figure 4.15).

Table 4.5 Seed rain DCA ordination summary

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.801	0.523	0.334	0.150
Gradient length	2.861	3.181	1.597	2.594
Cum. % variance	19.7	32.6	40.9	44.6

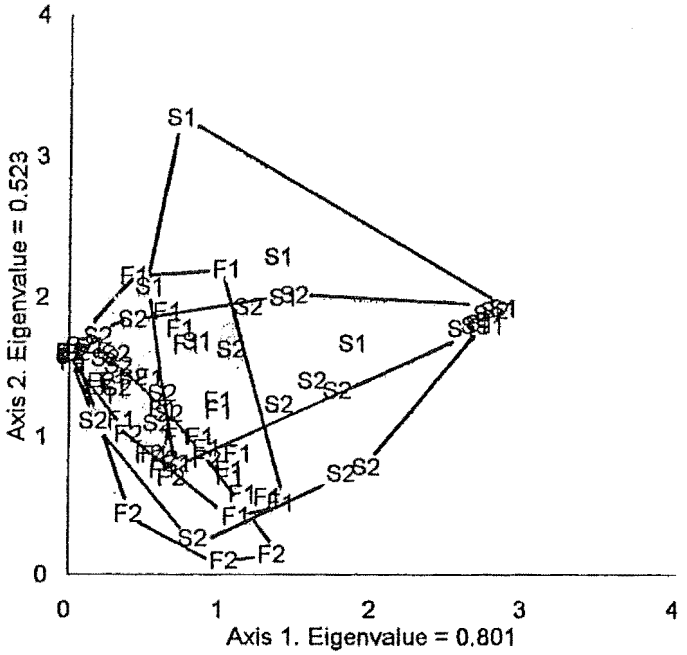

Figure 4.15. Scatter plot of DCA ordination site scores. Seed rain data

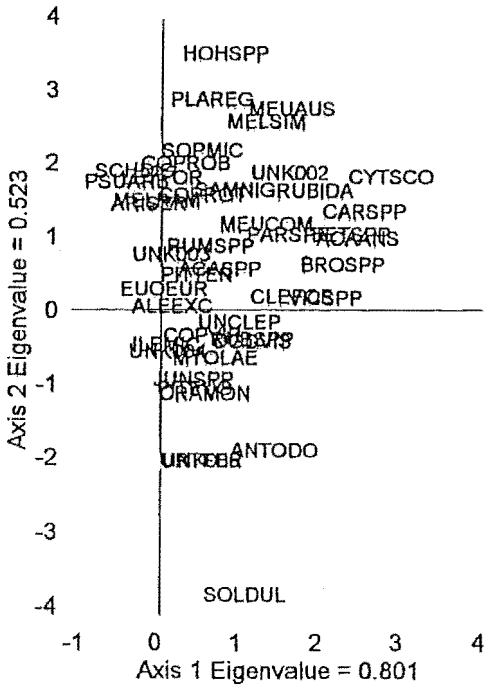

Figure 4.16. Scatter plot of DCA ordination species scores. Seed rain data

The way in which the site DCA ordination is being determined by species composition is further indicated by correlations of individual species seed rain at each site with site DCA axis position. As Table 4.6 shows Axis 1 is arranged on a gradient with species typical with forest habitat types at one end (*Clematis*, *Myoporum*, *Dodonea*) and species typical of scrub types at the other (*Cytisus*, *Mueuhlenbeckia*, *Hoheria*). A stronger forest-scrub gradient is indicated by Axis 2 correlations, which have mahoe at one end and broom at the other. These are the two indicator species used to separate forest and scrub types in the TWINSPAN ordination of Chapter 3.

Table 4.6 Pearson product moment correlation coefficients (*r*) for individual species seed rain counts and DCA ordination axis position (first two axes only). Only species with $|r| > 0.25$ tabled.

AXIS 1		AXIS 2	
CLEFOE	-0.49	MELRAM	-0.39
MYOLAE	-0.43	SAMNIG	-0.35
DODVIS	-0.36	CYTSCO	0.67
COPVIR	-0.35		
RUBSPP	-0.35		
UNCLEP	-0.33		
MEUCOM	-0.26		
CYTSCO	0.27		
MEUAUS	0.40		
HOHSPP	0.46		

iii. Seed rain diversity

The species diversity of the seed rain was calculated using the Shannen Weiner diversity index (Defined in Chapter 3), and an average diversity for each of the four habitat types obtained. These were significantly different at the 95% level (Table 4.7).

Table 4.7. Mean Shannen-Weiner diversity indices for total whole-seed rain of each of the four habitat types.

	S1	S2	F1	F2	F	*p*	Sig.?
Mean	0.756	1.575	1.145	1.167	11.51	<0.001	✓
s.d.	0.416	1.042	0.562	0.574			
Duncan's[1]	B	A	AB	A			

[1] Note: Habitat types with the same letter are not significantly different at the 95% level.

A Duncan's Multiple Range test indicated no significant difference in species diversity between types F2 and S2 at the 95% level (Table 4.7). These two were significantly different from type S1, although type F1 was not different from either S1 or F2/S2.

2. Seeds In Possum Faecal Clumps

Discrete faecal clumps of the brush tail possum were obtained in 79 out of 621 (ca. 13%) valid trap clearances. The number and species of whole seeds extracted from the aggregated faecal clumps are tabled below (Table 4.8)

Table 4.8. Whole seeds obtained from faecal clumps in each of the four habitat types. Data from 79 aggregated faecal clumps.

Species	S1	S2	F1	F2	TOTAL	%
MELRAM	56	3518	2289	770	6633	55.68
SAMNIG	693	2439	809	536	4477	37.58
ARISER		440			440	3.69
MEUAUS	79	110	14		203	1.70
MYOLAE		16	96	11	123	1.03
COPROB		8	5		13	0.11
LEYFOR			8		8	0.07
UNCLEP			6		6	0.05
CYTSCO	1	3			4	0.03
ALEEXC				1	1	0.01
ANTODO		1			1	0.01
COPVIR				1	1	0.01
PARSPP			1		1	0.01
PITTEN		1			1	0.01
TOTAL	**829**	**6541**	**3223**	**1319**	**11 912**	**100**
%	**6.95**	**54.91**	**27.06**	**11.07**		**100**

11 912 whole seeds from 15 predominantly woody species were obtained. Seven of these species are of the 11 most abundant seed species (Table 4.2), and together these contribute 95% of the total faecal seeds. Two species combined (mahoe and elder) contributed 92% of the total possum dispersed seed rain (56% and 36% respectively).

Possum dispersed seed rain differed significantly between habitat types (Table 4.7), as did the total possum faecal weight. A Duncan's multiple range test however was unable to separate the habitat types based on either of these.

Table 4.9 Weighted mean total faecal aggregate weight (seeds + other material) and number of whole seeds extracted from faecal aggregates. Differences between habitat types.

	S1	S2	F1	F2	F	*p*	Sig.?
Weight	0.801	1.322	0.866	0.243	6.87	<0.00	✓
Duncan's[1]	A	A	A	A			
Seeds	19.43	122.6	80.55	28.50	7.97	<0.00	✓
Duncan's	A	A	A	A			

[1] Note: Habitat types with the same letter are not significantly different at the 95% level.

There was no relationship between total aggregate weight and the number of seeds contained within (Least Squares Regression: seeds = 29.8weight + 96.24, r^2 = 0.02), even when observations were separated by month. This may be due in large part to the fact that damaged seeds were not able to be effectively separated from the other faecal material, and so differences in the number of seeds damaged by possum consumption may be obscuring other relationships. However both the total faecal aggregate weight and the number of possum-dispersed seeds varied significantly with month of observation (Faecal weight F = 3.99, p < 0.00; number of seeds F = 2.60, p = 0.04, Figure 4.17)

Both total faecal weight and number of faecal seeds follow approximately the patterns of total seed fall presented in Figures 4.3. However the relative importance of seed (and presumably fruit) in the diet of possums apparently shows a distinct peak. Figure 4.18 shows the proportion of seeds in the aggregated faecal clumps by weight, with a distinct peak in March, indicating that fruit and seeds are an important source of food over this time. This is presumably related to fruit availability, and as the diet of possums in Hoon Hay Valley has been the subject of concurrent research (O'Cain 1997) the implications of this for possum diet are discussed no further here.

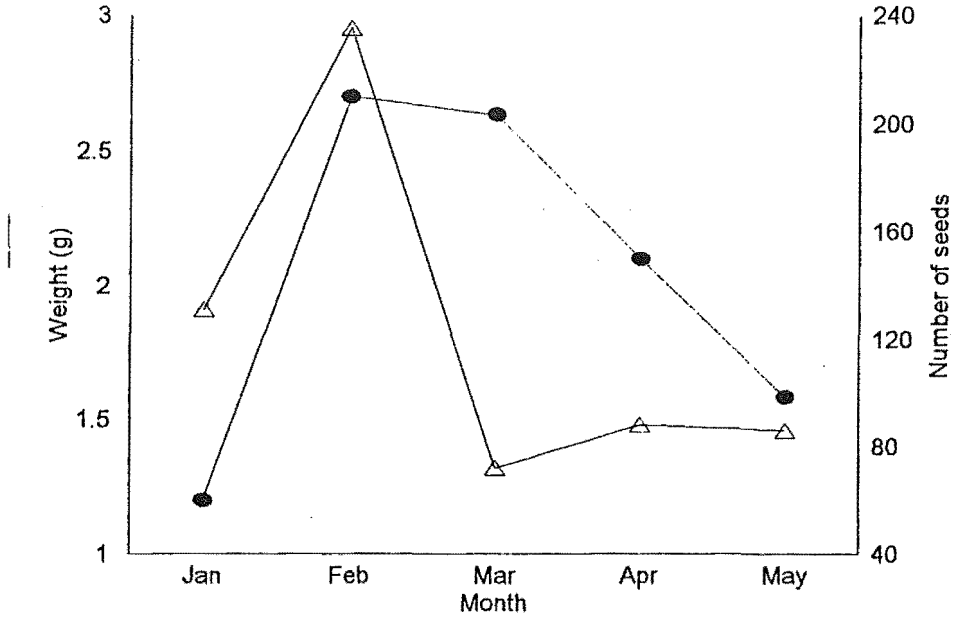

Figure 4.17 Relationship between total possum faecal weight and number of possum dispersed seeds.
●= number of seeds Δ= faecal weight

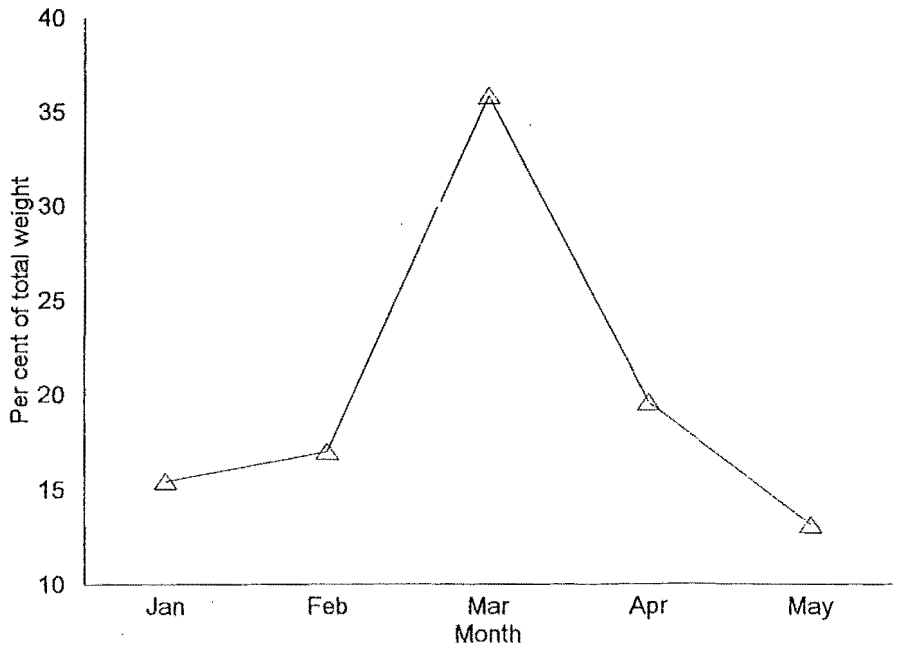

Figure 4.18. Seeds as a proportion of total faecal weight

3. Seed Predation

At the sorting stage any damaged seeds and fruit (apart from those in possum faecal clumps, which as described were treated seperately) were separated and where possible identified to species. The numbers of damaged seeds and fruit for each species are presented in Table 4.1, and the proportion of damaged seed for each of the 11 most abundant species is summarised in Table 4.10. Seed predation (% total seeds damaged) was 10.52% overall, and 13.15% for the 11 most abundant species.

Table 4.10. Seed predation (per cent of total seedfall which was damaged) for 11 most abundant seed species, Hoon Hay Valley, January - May 1996.

Species	% damaged seed
HOHSPP	69.97
DODVIS	49.69
MELRAM	10.52
PARSPP	8.09
CLEFOE	2.58
CYTSCO	2.41
COPVIR	2.28
SAMNIG	2.06
LEYFOR	0.00
ARISER	0.00
MEUAUS	0.00

4. Litterfall

The total dry-weight of litter (leaves, twigs, frass, invertebrates etc.) was measured. There was a significant difference in total litterfall between each of the four habitat types ($F = 11.89$, $p<0.00$). Litterfall in each of the habitat types was significantly different throughout the trapping period (Table 4.11). The habitat type in which the maximum litterfall occurred was different at each trap date, although the maximum was confined to only two habitat types (F2 and S2).

There was no relationship between the mass of litterfall and the mass of seeds and fruit observed (Least Squares Regression; seeds = 0.12.litter + 1.82, $R^2 = 0.07$); as Figure 4.19 shows litterfall is at a maximum near the start of the trapping period, and declines to a minimum near the end of the period, whereas the reverse is true for seed rain (Figure 4.2).

Table 4.11. Mean litterfall weight (grams, seeds + other material) between habitat types by trap date.

Day	S1	S2	F1	F2	F	*p*	Sig.?
24	3.06	4.74	3.55	4.94	5.66	<0.00	✓
43	6.63	7.87	5.77	5.87	7.66	<0.00	✓
57	3.02	5.21	3.18	2.78	15.16	<0.00	✓
71	3.19	5.52	4.82	6.35	8.83	<0.00	✓
85	1.99	3.15	1.89	2.52	7.39	<0.00	✓
101	1.82	2.87	1.54	3.22	5.92	<0.00	✓
114	1.42	2.98	2.18	4.22	4.80	<0.00	✓
141	2.58	6.30	4.12	5.47	5.98	<0.00	✓

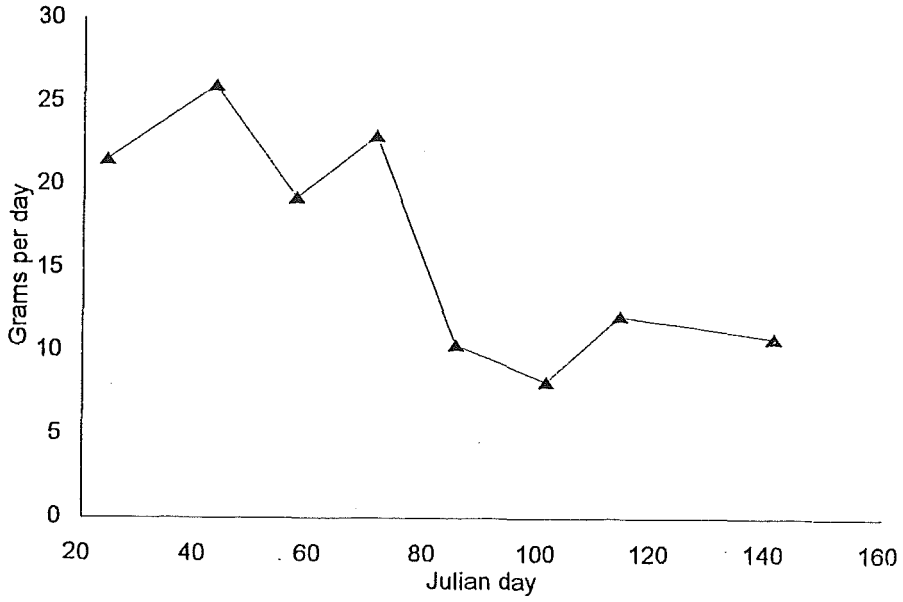

Figure 4.19 Temporal litterfall distribution

4. DISCUSSION

1. Error And Bias

There are several sources of potential error or bias associated with the results presented above, and implications of these deserve consideration prior to discussion of results in any detail. Firstly there will have been bias associated with the design of the seed traps used. The shade cloth material used was of a woven construction, and it is likely that the size of the holes in the weave was larger than the size of the smallest seed possibly encountered in the seed rain. The individual seeds of *Fuchsia excorticata* are significantly smaller than 1 mm in diameter (probably the smallest seeds encountered in the seed traps) and it is possible that had any entered the traps they may have fallen through gaps in the weave of the cloth. Given that no *Fucshia* seeds were counted, it is not known if this occurred, and there is no way of knowing with any certainty if any *Fuchsia* seeds would have been caught had the trap material been of a narrower mesh size. The largest hole in the trap material was larger than 1 mm in width, but given the tight bunching of tied material in the bottom of the traps the diameter of the smallest hole would have been significantly less than this, and so may have stopped very small seed from falling through the material. It is worth noting that the seeds of *Leycesteria formosa* are often smaller than 1 mm, but that these seeds were caught in the traps in significant numbers. In any case, given that *Fuchsia* was a minor contributor to the overall biomass measured in Chapter 3, and that essentially no *Fuschia* were observed immediately adjacent to seed traps, it is thought that the numbers of *Fuchsia* seeds potentially dispersed into the seed traps would be low.

Secondly it is possible that seeds and other material may have been predated in the traps prior to collection, or in the paper bags once samples had been taken back to the laboratory. The extent to which this occurred is unknown, and essentially un-quantifiable. Invertebrate predation of seeds and fruit in the traps is a virtual certainty (*contra* Burrows (1994b)), whereas predation by vertebrates is possible, but unlikely. Rat or mouse predation was not indicated as there was no sign of faecal material in the traps. Possums on the other hand were definitely getting into the traps, as in several instances possum faeces were found in traps with no directly overhanging vegetation. Possums would probably not have eaten trap contents as they would not have found them palatable (M. O'Cain, pers. comm.). However it is possible that possums would have disturbed the trap contents, possibly removing some of them. Possum interference with seed and litterfall traps has been encountered in other studies (P. Clinton, NZFRI, pers. comm.), but the extent to which this occurred in the present study remains un-

quantifiable without direct observation of possum behaviour. In accepting this as a source of error which is unlikely to adversely effect the overall study one relies on the tacit assumption that if possums are interfering with the traps than such interference is random, and equally likely in all the vegetation types. Again this is not able to be confirmed within the limits of the present study, and it is an assumption which is unlikely to be valid given the spatial variability in possum densities and behaviour observed in Hoon Hay Valley (O'Cain 1997) and indicated by the between-habitat type differences in possum faecal seed rain presented above.

It is also possible that wind dispersed seeds (e.g. of *Clematis* and *Parsonsia*) may have been blown out of the traps after they had been deposited - seed of these species are highly mobile and can be shifted with the slightest breeze. The extent to which this removal occurred is low as the feathery dispersal parts of these seeds readily inter-mesh with the woven trap material and can become somewhat firmly lodged in the traps.

A further source of error may have arisen as a result of trap emptying. It is possible that as material was transferred from the traps into the paper bags used for subsequent transport and storage some seeds would have escaped. Every effort was made to reduce the risk of this occurring, as traps were emptied over a sheet of plastic, and any material which fell out of the traps would have been caught on the plastic, and thence transferred into the paper bags.

Perhaps the most significant source of bias is in the overall experimental design, and in particular the duration of seed trapping. As described in the Method traps were installed in the first week of January, and were cleared until May on the assumption that essentially all of the seed fall would have occurred within that time. In respect of the majority of species this was a valid assumption (see Figures at the start of this Chapter), but in the case of two significant exceptions, mahoe (Figure 4.4) and *Parsonsia* spp. (Figure 4.9) it was not, as in both instances the maximum observed seedfall occurred at the last trap clearance date. It is not possible to say how many seeds would have been collected after the cessation of trap clearance, or how much this would influence the results presented here. The short duration of this study, necessitated by the time constraints of a short-term project, represent its weakest link, and the implications that this has for the validity of the overall study are discussed further in Chapter 6.

2. General Discussion

As presented in Table 4.1, 60 764 whole seeds from 46 predominantly woody plant species were trapped and identified, with an average seed rain density of 3875 whole seeds m^{-2} for the five months of seed trapping. Seed rain densities range from much less

than 1 seed m^{-2} for the species with only one or a few seeds caught, to in excess of 2000 seeds m^{-2} for the most abundant seed species (mahoe). In comparison Sem and Enright (1996) report 15 month seed densities of 2020 seeds m^{-2} (202 ± 93 seed per 0.1 m^{-2}) for 40 species in a temperate rainforest in the Waitakere ranges near Auckland. Beveridge (1964) reports seed rain densities for rimu (*Dacrydium cupressinum*) ranging from 52 - 345 seeds m^{-2} $yr.^{-1}$ and densities for miro (*Prumnopitys ferruginea*) of 695 seeds m^{-2} $yr.^{-1}$. Wardle (1984, and references therein) reports seed rain densities for beech (*Nothofagus*) species with an annual average of between 1000 and 2000 seeds m^{-2} $yr.^{-1}$, depending on species and location. Wardle (1970) reported seed rain densities of *Nothofagus solandrii* in the Kaweka ranges ranging from less than 1 seeds m^{-2} $yr.^{-1}$ to in excess of 13 000 seeds m^{-2} $yr.^{-1}$. Allen and Platt (1990) reported an average seed rain density of ca. 1500 seeds m^{-2} $yr.^{-1}$ for *N. solandrii* in Canterbury.

Seed rain has been investigated in numerous international studies. Herrera *et al.* (1994) investigated recruitment of a mast-fruiting bird dispersed tree (*Phyllyrea latifolia*) in a Mediterranean forest and scrubland and observed seed rain densities averaging 5.39 seed m^{-2} $yr.^{-1}$. Only one species was investigated, which exhibits high inter-annual seed rain variation. The authors describe the study interval as a mast year even though the seed rain for this species is low compared with species in the present study and others considered above. Mediterranean scrub also features in the work of Debussche and Isenmann (1994). They reported seed rain densities for each of 38 fleshy fruited species ranging from 354 to 1790 seeds m^{-2} $yr.^{-1}$. Shibata and Nakashizuka (1995) report seed rain densities for four co-occurring *Carpinus* species in a Japanese temperate deciduous forest. Over the 5 years of the study seed rain average 6.65 seed m^{-2} $yr.^{-1}$ for the four species combined, but there was significant inter-annual variation. Seed rain for *C. laxiflora* for the 5 years 1987 - 1991 was 0, 43.13, 0, 6.28, and 0.09 seeds m^{-2} $yr.^{-1}$ respectively.

The seed rain density observed in Hoon Hay Valley fall within the ranges of the sample of studies presented above. It is however difficult to adjust published results to be directly comparable with the 5-month study presented here. While it is tempting to derive a monthly average for each of the published studies and compare them on the basis of this, this would most likely lead to spurious comparisons being made as none of them produce monthly figures by which the temporal distribution of seed rain can be assessed. As this study sampled only the 5 months of maximum seed rain, calculation of a monthly mean would over-estimate annual seed rain densities and make direct numerical comparison with other studies difficult.

The most fruitful source of information for comparison is the work of C. J. Burrows in Ahuriri Summit Bush Scenic Reserve (Burrows 1994b, hereafter referred to as Ahuriri

Bush). As part of a long-term investigation of the seed biology of Banks Peninsula, Burrows has published research investigating the seed rain of Ahuriri Bush. Ahuriri Bush is a scenic reserve ca. 3 kilometres to the south of Hoon Hay Valley on the upper Port Hills (NZMS 260, M36/795272). It is an approximately 5 hectare forest remnant, and is one of the few surviving forest patches on Banks Peninsula which is in a relatively unmodified state. Logging and fire affected the reserve around 100 years ago, but as the forest has regenerated vigorously since then it represents a working model for the type of vegetation which might have been present in much of Hoon Hay Valley in pre-European times. Burrows (1994b) provides a thorough description of the vegetation on the reserve, and the most notable differences between that and the vegetation of Hoon Hay Valley are the presence of large mature podocarps in the canopy, and abundant *Fucshia excorticata*, *Grisilinea littoralis*, *Pseudopanax crassifolius*, and *P. arboreus*.

Burrows deployed an array of 16 seed traps was within a 25 x 25 m quadrat in the Reserve, and seed rain was monitored monthly for the 23 months of January 1985 to December 1986. The detailed results of this are presented in Burrows (1994b). Burrows separates the two years as more traps were added in 1986, and for the sake of simplicity only the 1985 data are considered here. A total of 17 648 seeds were trapped during 1985 from 24 species, to give an average (±1 s.d.) of 1103 ± 717 seeds per trap for the year. The catch area of each trap was 0.100 m^2 (c.f. 0.196 m^2 in this study), and so average seed rain density was ca. 11 000 seeds m^{-2} for the year (c.f. 3875 seeds m^{-2} for the five months of this study). Ten species contributed at least 1% of the total seed rain, and these 10 species combined contributed 94% of the total seed rain (Table 4.12)

Table 4.12. Species contributing at least 1% of total seed rain in Ahuriri Summit Reserve, 1985 (From Burrows (1994b), Table 6). Species codes are defined in Appendix 3.

Species	Seeds	% Tot.
PSECRA	8120	46.14
FUCEXC	2571	14.61
MELRAM	1816	10.32
PSUCOL	879	4.99
ARISER	849	4.82
LEYFOR	767	4.36
SCHDIG	496	2.82
HOHSPP	378	2.15
PSUARB	344	1.95
PITEUG	317	1.80
Total	**16 537**	**93.97**

As with the present study seed rain was highly variable, with significant differences between traps and between the two years of published trap monitoring. Burrows cites several factors which contributed to this variability, all of which are dealt with in respect

of the variability observed in the present study in the proceeding discussion. Burrows made observations of the fruiting phenologies of individuals in the 25 x 25 m quadrat (qualitative details of which he appends), and makes the observation that conspecific individuals can vary widely in their fruit production at any one time.

Comparison of the present study with the results of Burrows (1994b) yields some interesting results. Firstly seedfall was substantially higher in Ahuriri Bush than was observed in Hoon Hay Valley. For 48 woody species the 12 month average was 11 154 seeds m^{-2} $yr.^{-1}$, compared with a third of that for the 5 months of the present study (3875 seeds m^{-2}). This difference may be related to the different species present in the two study areas. The two most abundant seed species in Burrows' work are either absent (*Pseudopanax crassifolius*) or significantly less common (*Fuchsia excorticata*) in Hoon Hay Valley. These two species together contribute ca. 6700 seeds m^{-2} $yr.^{-1}$, which is greater than all the seeds trapped during 5 months of trapping in the present study. These two species are apparently quite abundant in the vegetation in Ahuriri Bush, so it would be interesting to see what effect they would have on seedfall in Hoon Hay Valley if they were present in similar quantities.

The differences in seed rain between Ahuriri Bush and Hoon Hay Valley are however difficult to assess in anything other than a qualitative fashion, as Burrows has not quantitatively related seed rain to the vegetation present in the Reserve. The relative basal area and heights of each of the individuals present in the 25 x 25 m quadrat are given, but these are not related to canopy extent, or any other means of quantitatively estimated fruit production. Burrows states that the quantity of seed rain is directly related to the overhanging vegetation in terms of fruit production (Burrows 1994b, p.194), but the nature of this relationship is not able to be described with the information published.

Given that the overall trapping period was longer in the Ahuriri study the most useful comparisons relate to the temporal distribution of seedfall. Burrows noted that although there was a general seedfall trend with greater seedfall occurring in the autumn months (March-May), the periodicity of seedfall was highly species-specific. Most of the abundant species had a peak seed rain period over 1-3 months in late summer and autumn, with a few species having a lengthy period of seedfall over 4-5 months. The individual patterns showed no clear systematic trend, although Burrows makes a distinction between those species with seedfall peaks in February (summer), March to May (autumn), and June-August (winter). He surmises that these inter-species differences are genetically inherited responses to climate-mediated growth cues, particularly at the time of flower and bud initiation. This observation aids interpretation of Figures 4.4 to 4.14 which indicate that all species have distinct temporal seed rain

patterns. The majority however have maxima in either summer or autumn, and so few seed species trapped in Hoon Hay Valley could be considered winter species. As noted previously the short time of seed trapping in the present study prevents definitive conclusions about the year-long temporal patterns of seed rain in Hoon Hay Valley. It is however possible to conclude that for all but two of the most abundant seed species (mahoe and *Parsonsia* spp.) the majority of seed rain occurs in late summer or autumn, which supports the observations of Burrows in Ahuriri Bush.

It is possible that continuing seed trapping further in the present study may not have yielded significantly more information on temporal seed rain trends. It is apparent that many plant species commonly exhibit very wide inter-annual variability in seed production (Wardle 1970, Harper 1977, Silvertown 1980, Norton and Kelly 1988, Allen and Platt 1990). Abundant seed production in many plants occurs synchronously at irregular intervals, and this phenomenon is usually called mast seeding (Silvertown 1980, Norton and Kelly 1988). Norton and Kelly (1988) cite several studies in which mast seeding has been observed in New Zealand species (Travers 1962, Beveridge 1973, James and Franklin 1978, West 1986, Wardle 1971, Haase 1986). It is not known if any of the species in Hoon Hay Valley exhibit mast seeding, and of the species present only the reproductive biology of one (*Melicytus ramiflorus*) has apparently been investigated in any detail (Powlesland 1984); no mention is made of observed mast fruiting behaviour, although mention was made of a wide variability in fruit production within a single fruiting season. Silvertown (1980) makes the observation that masting behaviour is more common in northern temperate woody species with non-fleshy rather than fleshy fruits, and Norton and Kelly (1988) suggest that economies of scale associated with synchronous periodic heavy flowering in wind pollinated species would tend to favour evolution of masting behaviour in these species. As most of the species in Hoon Hay Valley are fleshy fruited and not reliant on wind pollination it can safely assumed that mast fruiting is unlikely to be the proximate cause of inter-annual variation of fruiting and seed fall behaviour, and that temporal patterns of seed rain observed are driven by factors such as genetically mediated responses to climatic cues.

A. Spatial Pattern

As described above (Figure 4.2, Tables 4.3 and 4.4) seed rain density at each of the 80 seed traps varied by several orders of magnitude, ranging from 38 198 seeds m^{-2} at the most productive trap to less than 500 seeds m^{-2} at the least productive trap over the five months of the trapping period. It is also apparent that there are distinct spatial patterns in seed rain, with the four habitat types exhibiting significant differences in overall seed rain

density (Table 4.3) and diversity (Table 4.7). Significant between-habitat differences were also observed for the most abundant seed species (Table 4.4).
How can these spatial patterns be explained? Firstly spatial patterns of seed rain will be related to spatial patterns of fruit availability to seed dispersers in the case of species reliant on biotic dispersal, and spatial patterns of seed production for species reliant on abiotic dispersal. Given that the majority of seed is dispersed relatively close to the parent plant (Silvertown 1987, Harper 1977, Tilman 1988) it follows that one of the most significant spatial determinants of seed rain is the spatial pattern of seed availability. Different seed will be available in different vegetation, with seasonal/temporal differences active as well. This has particular importance when considering coupling of spatial patterns of vegetation and seed rain which is the first step of the conceptual recruitment pathway as described in Chapter 1. The implications of this for the spatial pattern of seed rain in Hoon Hay Valley are discussed in more detail in Chapter 6.

Secondly, patterns of seed rain will be influenced by the feeding choices of frugivorous dispersers. As mentioned in the introduction to this Chapter the majority of woody plant species present in the Valley are dependant on frugivorous birds for seed dispersal. The species of fruit preferred by dispersers will have implications for spatial seed rain pattern; those species preferentially targeted will have a greater chance of dispersal, although the effectiveness of this dispersal may vary depending on the frugivores present (Howe 1986, 1989, Clout and Hay 1989).

Fruit preferences and fruit availability are related to fruit conspicuousness, and the physical availability of fruit to dispersers present. Fruit conspicuousness is a function of the colour of fruit, particularly when contrasted against the background colour of foliage and bark (Lee *et al.* 1994), and the spatial presentation of fruit displays (Denslow 1987). Fruit colour has been investigated for a variety of fleshy fruited New Zealand species (Lee *et al.* 1988; Weatherall and Lee 1991; Lee *et al.* 1994), and it was observed that many of the fruits of bird dispersed species have colours tending toward the red end of the colour spectrum, or had fruit of dark colours. It was observed that these colours offer the greatest contrast against the green foliage and bark colours (Lee *et al.* 1994), particularly to diurnal avian frugivores. This interpretation has been confirmed for other temperate species and tropical florae (Willson *et al.* 1989, Willson and Whelan 1990). Most of the fleshy fruited species in Hoon Hay Valley have ripe-fruit colours which indicate that they are suited to bird dispersal, and so one would expect that patterns of seed rain are related to spatial patterns of bird feeding behaviour.

Spatial patterns of bird behaviour can have quite substantial impacts on spatial patterns of seed dispersal. It is apparently common for frugivorous birds to ingest fruit in one tree, and then fly away to digest and then defecate seeds (Howe 1986). This can have

significant implications for seed depositions, with many seeds deposited in beneficial habitats away from the parent tree. For example seedlings of podocarp species in forests of Westland are significantly correlated with overhead angiosperm canopy - the implication is that seed dispersers ingest podocarp seeds and fruit and then fly to nearby angiosperm species to perch where they digest the fruit and either regurgitate seed or void them in their faeces (Norton 1991, Clout and Hay 1989). Burrows (1994) observed similar patterns of seed deposition, with significant clumps of deposited seed beneath known kereru perch sites, and large numbers of seed deposited on fence posts and perch sites of other frugivorous birds. Frugivore movement such as this may be a response to preferred perch sites, or as a mechanism to avoid predators (Howe 1986).

Feeding behaviour may also be related to the accessibility of fruit to birds. For example Moermond and Denslow (1983) showed that small differences in fruit accessibility from a bird's perch site could significantly override preferences for fruit type, ripeness, and colour. A similar result was observed by Moore and Wilson (1982). Fruit preferences are related to many other factors, such as gape size (e.g. Williams and Karl 1996), digestion physiology (e.g. Martinez del Rio and Restrepo 1993), and gut morphology (e.g. Courtney and Sallabanks 1992). Direct consideration of these factors is important in determining disperser/dispersal behaviour on a per-species basis, but does little to explain the spatial pattern of seed rain observed in this study.

These factors combine to create at-times large differences in seed rain between habitat types, and it is probably the interaction of all these which is driving the observed spatial pattern of seed rain in Hoon Hay Valley (e.g. Table 4.3, 4.7, Figure 4.15). Support for this assertion is provided by Herrera *et al.* (1994). In a study of seed dispersal of *Phillyrea latifolia* (a mast seeding Mediterranean forest tree species) Herrera *et al.* (1994) observed that seed rain varied widely depending on habitat type, and that this was due in large part to the behaviour of frugivorous birds. They observed greater removal of fruit in habitats with a greater abundance of dispersers, whereas the influence of disperser abundance on removal within each habitat types was negligible. Total seed rain in the habitat types was significantly correlated with percent cover of *P. latifolia* which produced more than 80% of the total seedfall. The structure of overlying vegetation accounted for a significant portion of the total variation in seed rain. Seed rain was observed to be greatest at the interface between complex and simple vegetation compared with seed rain at either forest interior or open sites. Differences were also observed between vegetation patches of differing successional status.

Frugivore mediated differences in seed rain between patches of differing structural complexity have been observed in other studies. Debussche and Isenmann (1994) report significant associations between canopy height and seed rain in patchy Mediterranean

scrub, with tall and isolated trees acting as recruitment foci, beneath which large quantities of seed are deposited. McDonnell and Stiles (1983) observed that seed rain was directly related to the structural complexity of vegetation. As in the study of Herrera *et al.* (1994) seed rain was significantly higher at the interface between patches of differing complexity than beneath either closed forest or open sites, and the movement of birds between differing habitat patches had significant implications for seed rain patterns. Structurally simple vegetation had a relatively low seed rain, but this was increased by the introduction of artificial complexity in the form of artificial structures shaped to resemble shrubs or small trees.

The importance of structural complexity in mediating spatial seed rain patterns in successional environments similar to that in Hoon Hay Valley has been emphasised by McClanahan and Wolfe (1993), and Robinson and Handel (1993). Both these studies report that dispersal of seed into deforested ecosystems is enhanced by increases in structural complexity altering avian disperser behaviour (see also Robertson and Hackwell 1995). McClanahan and Wolfe (1993) report that restoration sites with artificial perch sites (*sensu* McDonnell and Stiles 1983) experienced seed rain densities 150 times greater than those without. Seed dispersed around preferred perch sites can have significant implications for succession. Yarranton and Morrison (1974) observed that preferred perch trees can provide foci about which succession is concentrated. Robinson and Handel (1993) reported that an increase in structural complexity associated with a restoration planting had the result of increasing recruitment of fleshy fruited species from outside the planted area to the point where only one year after planting 95% of fresh seedlings were sourced outside the planted area.

These studies indicate that seed rain is greatest in structurally complex vegetation. As described in Chapter 3 the vegetation of Hoon Hay Valley is a complex mosaic of successional species with habitats exhibiting a high degree of internal spatial heterogeneity. Although differences in seed rain between forest (F1/F2 combined) and scrub (S1/S2) are not significant, there are significant differences in seed rain between the four individual vegetation types (Table 4.3). These can be related to spatial patterns in vegetation structure by comparison with Table 3.5 of Chapter 3. As Table 3.5 describes there are significant differences in spatial allocation of biomass between the four habitat types considered in this study. The forest types contain both greater standing biomass (as measured by their vegetation scores) and greater structural complexity as measured by the standard deviations of their vegetation scores. A direct comparison of structural complexity and seed rain patterns yields interesting results (Table 4.13)

Table 4.13. Comparison between habitat types of biomass and seed rain density. Biomass data is from Table 3.5, and seed rain data from Table 4.3.

	BIOMASS		SEED DENSITY		SEED DIVERSITY	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
S1	150.53	60.62	281	321.17	0.756	0.416
S2	190.35	68.38	1220.93	1684.5	1.575	1.042
F1	231.05	83.57	547.43	680.08	1.145	0.562
F2	231.05	96.31	501.60	316.42	1.167	0.574

Given the results of the studies presented above one would expect seed rain density and diversity to follow patterns of spatial variability in habitat structure, and that the habitat type with the greatest seed rain density and diversity would be the same as the one with the greatest biomass and structural variability. However as Table 4.13 indicates this is not the case as the habitat type with the greatest seed rain density and diversity (S2) does not have the greatest biomass or structural diversity (as measured by the standard deviation of the biomass score). This is an apparently confusing result given the consistent trend of the published studies mentioned above. The basis of Table 4.13 comparisons can be questioned, particularly in respect of the assumption that standard deviation of mean biomass score is a valid measure of structural complexity. If this assumption is valid, the lack of a result consistent with the above mentioned studies indicates that the structural complexity of vegetation is not the most important determinant of seed rain density or diversity, or that other factors are obscuring this trend. The trend is however confirmed by consideration of the scrub habitat types alone, in which case the habitat type with the greatest vegetation structural complexity *does* have the greatest seed rain density and diversity; S2 has significantly higher structural complexity than S1, and a very much larger seed rain density and diversity. That the same trend is inverted for the Forest types indicates that patterns are not simple, and possible reasons for this are not forthcoming on the basis of results reported in this Chapter. A more detailed investigation of overall spatial pattern relies on further comparison with vegetation composition, which is dealt with in more detail in Chapter 6.

B. Possums As Seed Dispersal Mutualists

One of the more interesting results of this study is the observation of dispersal of seed by possums, and it is apparent from Table 4.6 that this is a significant part of seed dispersal in Hoon Hay Valley. Non-possum dispersed seeds totalled 60 764 whole seeds, and possum dispersal adds a further 11 912 seeds to this total. The total whole seed rain is thus 72 676 whole seeds, of which possums contributed just over 16%.

O'Cain (1997) presents the results of a concurrent investigation of possum diet in Hoon Hay Valley in which fruit and seeds contributed a highly significant proportion of possum diet (Table 4.14).There were significant differences between seasons and vegetation types in diet composition, but fruit and seeds together comprised almost 70% of total possum diet. It is interesting to note that seeds comprised less than 1% of the total annual diet, even though this consumption comprised a substantial proportion of total Valley seed rain. Given that the results presented in Table 4.14 are for undigested stomach contents the difference in the relative proportions of seeds and other material between Tables 4.14 and 4.8 is a reflection of normal possum digestion. O'Cain (1997) was able to separate fruit to species in gut content analysis, and the results of this are presented in Table 4.15

Table 4.14. Per cent dry weight contribution of main food groups in possum diet, Hoon Hay Valley. From O'Cain 1997, Table 4.8

	Summer	Winter	Annual
Fruit	79.5	0.76	69.2
Foliage	14.7	96.5	25.6
Wood	3.92	0.09	3.41
Invertebrates	0.77	0.09	0.68
Birds	0.45	0.00	0.39
Flowers	0.00	2.50	0.33
Unidentified	0.23	0.00	0.20
Seed	0.17	0.05	0.15

Table 4.15. Total per cent dry weight of identified fruit species in possum diet, Hoon Hay Valley. From O'Cain (1997), Table 4.11.

Fruit species	%
Sambuccus nigra	34.68
Melicytus ramiflorus	29.93
Myoporum laetum	11.83
Solanum aviculare	11.00
Meuhlenbeckia australis	8.20
Rubus fruiticosa agg.	3.75
Fuchsia excorticata	0.40
Pennantia corymbosa	0.08
Pittosporum tenuifolium	0.01
Unknown	0.03

As with Table 4.8 the majority of fruit is from two species, *Sambuccus nigra* and *Melicytus ramiflorus* indicating that these are preferred species in possum diet. O'Cain (1997) observed significant between vegetation type and season differences, some of which were mediated by aspects of possum foraging behaviour. It is however clear from results presented in Tables 4.14 and 4.15 that fruit comprises a significant proportion of possum diet, and that associated seed processing by possums comprises a substantial proportion of total Valley seed rain.

It has been apparent for some time that possums eat a significant quantity of fruit (Williams 1982, Coleman *et al.* 1985, Cowan 1990, Cowan and Waddington 1990, Owen 1993, Owen and Norton 1995). This has not often been interpreted in terms of effective seed dispersal, and even in other studies of seed dispersal in New Zealand forested areas the importance of possums as seed dispersers has been downplayed (e.g. Burrows 1994b). Given the ubiquitousness of the possum in New Zealand forests, and the importance of fruit and seeds in possum diets as presented here and by O'Cain (1997), this is a curious omission.

Cowan (1990) investigated the contribution of fruit, seeds, and flowers to the diet of possum in some detail for a possum population in a mixed angiosperm-podocarp forest in the Orongorongo Valley. The fruit and seeds of 18 predominantly fleshy fruited species were observed in possum faeces, with species composition related directly to fruit availability. No quantitative assessment was made of the implications that this frugivory would have in terms of overall seed rain, although Cowan made the observation that seed dispersal by possums may be of particular importance to native plant species with large seeded fruits; extinction or marked decline in numbers of large frugivorous birds may have left these species with a reduced native disperser assemblage (see also Clout and Hay 1989).

The importance of possums as seed dispersers has been indicated in studies in Australia. Bass (1990) reported that possums were important seed dispersers of the introduced weed tree *Crataegus monogyna* (hawthorn) in Australia. Faecal analysis (similar to that conducted in this study) revealed that possums were ingesting and dispersing significant numbers of hawthorn seeds. Viability of ingested/dispersed seeds was essentially the same as that for non-ingested seed, indicating that gut passage through possums does not have a negative effect on the germinability of this species. Bass (1990) made the interesting observation that fruit ingestion was not incidental to foliage consumption (as has been suggested in other studies (e.g. Cowan 1990)) as hawthorn is deciduous and thus without foliage for most of the fruiting season. Bass (1990) concluded that the role

of possums in dispersal of fleshy fruited species both in New Zealand and Australia, and particularly in investigations of plant invasions should not be overlooked

Seed dispersal has been observed by previously unsuspected mammalian dispersers in other studies. Willson (1993) investigated frugivory and seed dispersal by predominantly carnivorous mammals in North America, and Herrera (1989) reported effective seed dispersal by carnivores in Mediterranean forest vegetation (see also Debussche and Isenmann (1989)). Zedler and Black (1992) observed rabbits dispersing significant quantities of seed in a semi-arid Californian vernal pool landscape, although they suggested that any positive effects of rabbit seed dispersal were outweighed by the negative effects of herbivory.

Possums are definitely important dispersers of seed in Hoon Hay Valley. While no assessment was made of the germinability of possum dispersed seeds in this study the results of Burrows indicate that provided no direct mechanical damage of seeds occurs during digestion, and germination should proceed once parental tissues have been removed (but note Beveridge (1964) who observed seed predation by possums in North Island podocarp forests). Given that possums dispersed around 16% of the total whole seeds their importance as agents of seed dispersal cannot be overlooked.

C. Seed Predation

As Table 4.10 indicates several of the woody plant species present in Hoon Hay Valley are subject to significant predation of seeds. Seed predation is apparently as high as 70% for *Hoheria*, and ca. 50% for *Dodonea viscosa*. Seeds of both these species have large papery accessory structures enabling dispersal by a combination of wind and gravity, and it is interesting to note that fleshy fruited species (which make up most of the rest of Table 4.10) have substantially lower seed predation than these two non-fleshy species.

Seed predation has been investigated in only a few New Zealand species, and where it has been discussed it is usually in respect of post-dispersal predation (e.g. Wardle 1984, and references therein). The only published account of pre-dispersal seed predation in the New Zealand flora is apparently that of Sullivan *et al.* (1995), who investigated insect predation of the fruit and seed of native New Zealand woody plants taken from a variety of central South Island locations. Nine tree species were more or less heavily predated by insects, with predation killing generally around 10% of seeds is most cases, and up to 63% in others. Of the species present in Hoon Hay Valley, predation results are presented for thirteen species, and the information presented by Sullivan *et al.* (1995) is summarised in Table 4.16.

Predation was observed to vary widely between species and locations, and some species had more than one predator. The range of seed predation observed in Hoon Hay Valley (Table 4.10) is apparently not inconsistent with the potential range of predation reported by Sullivan *et al.* (1995). The implications that this predation has for forest regeneration are not known, but given that even in the most severe seed predation years some seeds usually (but not always) escape, predation is not likely to have a substantially detrimental effect. Sullivan *et al.* (1995) indicate that as both fruit and seed productivity and the degree of infestation of predators are all quite variable from year to year the results they present should all be taken as indicative, and that further research needs to be undertaken before the implications of seed predation can be fully identified.

Table 4.16 Pre-dispersal insect predation of seeds and fruit of 13 species present in Hoon Hay Valley. From Sullivan *et al.*(1995) Table 1.

Species	Fruit %	Seed %	Predator
Alectyron excelsus		1-30	*Conomorpha cyanospila* (Lepidoptera)
Calystegia tuguriorum	23-57	47	*Stathmopoda skelloni* (Lepidoptera) *Bedellia somnulenta* (Lepidoptera)
Hoheria angustifolia	50-80	6-100	*Anisoplaca achyrota* (Lepidoptera)
Plagianthus regius		2	*Anisoplaca* sp. (Lepidoptera) *Peristoreus* sp. (Coleoptera)
Sophora microphylla		11-22	*Stathmopoda aposema* (Lepidoptera)
Clematis foetida	3		Unknown
Griselinea littoralis		1-35	*Heterocrossa* sp. (Lepidoptera)
Myrsine australis		3-7	*Microcolona limodes*
Solanum lacinatum	83	22	*Sceloides cordalis* (Lepidoptera)
Melicytus ramiflorus	1-38		*Dipterina imbriferana* (Lepidoptera) *Pyrgotis plagiatana* (Lepidoptera)

CHAPTER 5

SEEDLINGS

1. INTRODUCTION

Seedlings are the final link on the conceptual recruitment continuum. Factors associated with dispersal of seed discussed in the previous Chapter are given expression in germinating seedlings. As seeds represent the potential future vegetation at a site, germination and establishment of seedlings offer the first opportunity for vegetation change to be expressed. Examination of the patterns associated with seedling germination and establishment can provide important information on processes of vegetation change.

2. METHOD

To assess the distribution of seedlings present in Hoon Hay Valley an array of 80 1 m square quadrats was deployed, within which seedlings were identified and counted periodically. Each of the 80 quadrats was randomly located within a 5 m radius of the survey locations described in Chapter 3, with the proviso that quadrats were shifted if their random location coincided directly with the seed trap positioned at the same location, or if their location was such that access to the quadrat for measuring would have resulted in significant disturbance to the vegetation present. In such a situation it was thought that vegetation disturbance associated with periodic seedling counts would have altered the growing environment for the seedlings, thus introducing unnecessary bias. This however introduces bias of its own in that patches of ground beneath thick vegetation are under-represented in the sample.

Each quadrat consisted of two short wooden stakes hammered into the ground so that approximately 5 cm of stake protruded, and positioned such that they formed the diagonal corners of a 1 m by 1 m square. A 1 m square collapsible aluminium frame was then placed over the stakes and the seedlings (defined as individuals between 2 cm and 1 m in height) rooted within its boundaries identified to species and counted. Seedlings were not individually tagged, and the total number of seedlings of each species in each quadrat was counted three times during 1996, in February, June, and November, to give a total sample period of 9 months.

3. RESULTS

Seedlings from 32 predominantly woody species were observed and the total number of seedlings for each of the species counted at each census period, and the percent contribution they make to the total seedling population, is described in Table 5.1.

Table 5.1. Total Numbers of seedlings counted and percent of total for each of the measurement periods. Species codes are defined in Appendix 3.

	February		June		November	
Species code	No.	%	No.	%	No.	%
ARISER					1	0.04
CALTUG					14	0.51
CLEFOE	8	0.33	22	1.20	20	0.73
COPAER	4	0.16	6	0.33	3	0.11
COPCRA	47	1.94	9	0.49	15	0.55
COPROB	36	1.48	37	2.02	45	1.64
COPROT	284	11.71	108	5.90	188	6.83
COPVIR	25	1.03	56	3.06	73	2.65
CYTSCO	379	15.62	156	8.52	250	9.09
DODVIS	10	0.41	8	0.44	7	0.25
EUOEUR	26	1.07	15	0.82	36	1.31
FUCEXC	1	0.04			3	0.11
GRILIT	14	0.58	4	0.22	6	0.22
HOHSPP	231	9.52	152	8.30	116	4.22
LEYFOR	2	0.08				
MELRAM	212	8.74	20	1.09	250	9.09
MEUAUS	61	2.51	191	10.43	172	6.25
MEUCOM	25	1.03	70	3.82	5	0.18
MYOLAE	1	0.04	9	0.49	2	0.07
PARSPP	839	34.58	277	15.13	1275	46.35
PENCOR	31	1.28	53	29.00	35	1.27
PITEUG			20	1.09	13	0.47
PITTEN	100	4.12	104	5.68	154	5.60
PRUAVI					3	0.11
PSECOL					2	0.07
PSUSPP			3	0.16	2	0.07
RUBFRU	3	0.12	7	0.38	7	0.25
RUBSPP	20	0.82	3	0.16	3	0.11
SAMNIG	41	1.69	9	0.49	30	1.09
SOLLAC					2	0.07
SOPMIC	25	1.03	13	0.71	15	0.55
URTFER	1	0.04	1	0.05	4	0.15
TOTAL	**2426**	**100.00**	**1353**	**100.00**	**2751**	**100.00**
Per m^2	**30.33**		**16.91**		**34.39**	

1. Seasonal trends

The seasonal trend in seedling numbers is described in Figure 5.1, with a decrease in overall seedling numbers from summer to winter (February to June census), rising to a maximum in spring (November census). This overall trend is however not significant, as there is no significant difference in total seedling density between the census periods (Table 5.2).

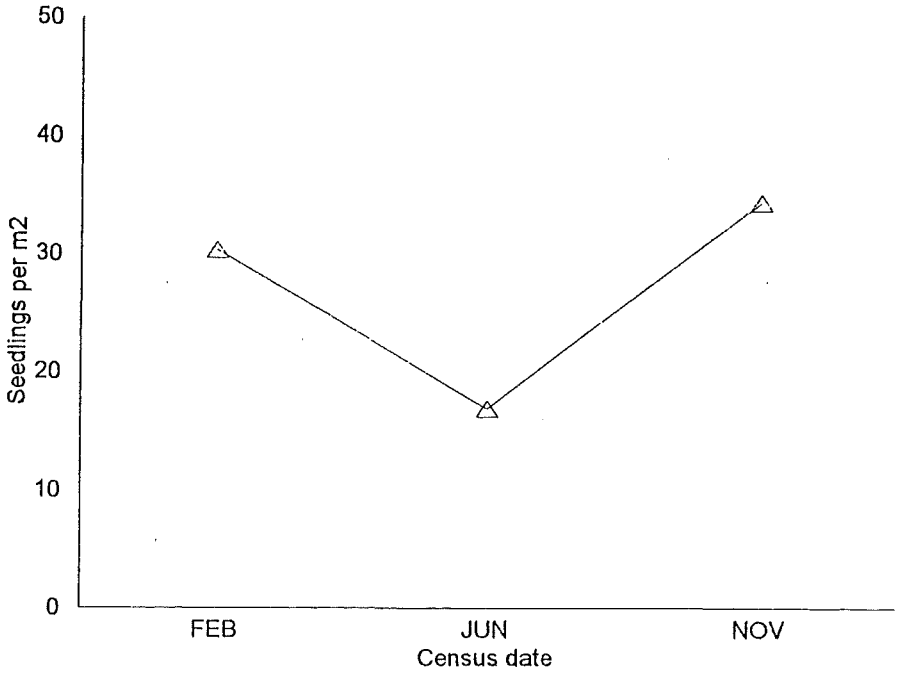

Figure 5.1. Seasonal trend in seedling density.

This non-significant result was constant even at the scale of the four individual habitat types (Table 5.2).

Table 5.2. Differences in mean seedling density (seedlings m^{-2}) at each season between habitat types

	February		June		November		F	*p*	Sig.?
	mean	s.d.	mean	s.d.	mean	s.d.			
Overall	30.33	34.21	22.89	25.81	34.39	35.38	2.56	0.08	No
S1	35.13	48.25	15.00	34.40	28.87	34.63	0.55	0.58	No
S2	32.63	28.50	23.74	21.31	32.81	29.52	1.02	0.37	No
F1	32.75	35.27	27.82	28.31	43.89	44.09	1.43	0.25	No
F2	10.10	6.98	11.10	6.56	20.30	14.51	3.14	0.06	No

Individual species exhibited different seasonal trends, although these were generally not significant (Table 5.3). A significant trend was observed for only 2 species, *Parsonsia* spp. and *Melicytus ramiflorus*.

Table 5.3. Mean seasonal seedling density (seedlings m^{-2}) for each of the 10 most abundant seedling species.

	FEBRUARY		JUNE		NOVEMBER				
	mean	s.d.	mean	s.d.	mean	s.d.	F	*p*	Sig.?
PARSPP	10.49	20.00	3.46	9.13	15.94	28.50	7.25	< 0.00	✓
CYTSCO	4.74	12.11	1.95	5.01	3.13	7.15	2.11	0.12	no
MELRAM	2.65	6.51	0.25	1.60	3.13	7.37	5.74	< 0.00	✓
COPROT	3.55	11.36	1.35	4.52	2.35	6.58	1.51	0.22	no
MUEAUS	0.76	1.84	2.39	7.40	2.15	5.36	2.13	0.12	no
PITTEN	1.25	2.46	1.30	2.24	1.93	2.74	1.83	0.16	no
HOHSPP	2.89	21.56	1.90	14.09	1.45	9.96	0.17	0.84	no
COPVIR	0.31	0.74	0.70	1.38	0.91	2.85	2.10	0.12	no
COPROB	0.45	1.65	0.46	1.71	0.56	2.10	0.09	0.91	no
EUOEUR	0.33	1.20	0.19	0.62	0.45	1.31	1.17	0.31	no

Tables 5.2 and 5.3 indicate a high degree of variability in seedling density (as measured by standard deviation of the sample mean) of both individual seedlings, and of seedling density between the vegetation types. In virtually all cases the observed standard deviation of mean quadrat seedling density is greater in magnitude than the mean in each of the populations. This is particularly relevant when considering the high *p*-values associated with the calculated F statistics (Tables 5.2 and 5.3). Virtually all the tests which do not reject the null hypothesis (i.e. that each of the habitat types has different seedling density) are associated with a high *p*-value. For example a *p*-value of 0.91 for *Coprosma robusta* in Table 5.3 indicates that there is a 91% chance that the result obtained (i.e. that there is no difference in seedling density between the habitat types) was arrived at by chance, rather than by any actual lack of difference between habitat types. This is most certainly associated with the wide standard deviations associated with each of the habitat-type means, and indicates that there is a high variability in seedling populations at the habitat level.

2. Spatial pattern

i. Seedling density

In spite of the lack of overall inter-seasonal difference there were significant differences in observed seedling density between each of the vegetation types, and these differences remained significant for each of the measurement periods (Table 5.4)

Table 5.4. Differences in seedling density (seedlings m^{-2}) between each of the four habitat types over the measurement period.

	S1		S2		F1		F2				
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	F	P	Sig.?
FEB.	35.13	48.25	32.63	28.50	32.75	25.27	10.10	6.98	5.69	0.00	✓
JUN.	20.00	34.4	23.74	21.31	27.82	28.37	11.10	6.56	6.65	0.00	✓
NOV.	28.87	34.63	32.81	29.52	43.89	44.09	20.30	14.51	7.86	0.00	✓

A significant difference in seedling density between each of the four habitat types was also observed for all but three of the most abundant seedling species (*Hoheria* spp., *Coprosma virescens*, and *Euonymus europeaus*) (Table 5.5), although once again all the non-significant results were associated with high *p*-values.

Table 5.5. Differences between habitat types in mean seedling density (seedlings m^{-2}) for the ten most abundant seedling species. November data only.

	S1	S2	F1	F2	F	*p*	Sig.?
PARSPP	1.07	17.52	26.46	4.50	8.35	0.00	✓
CYTSCO	9.27	13.56	0.54	0.00	4.45	0.01	✓
MELRAM	1.73	4.74	3.36	0.20	3.19	0.03	✓
COPROT	0.07	2.30	4.21	0.70	3.58	0.02	✓
MUEAUS	8.33	0.56	0.89	0.70	5.73	0.00	✓
PITTEN	0.73	1.19	2.07	5.30	2.85	0.04	✓
HOHSPP	6.07	0.15	0.61	0.40	0.86	0.46	no
COPVIR	0.47	0.26	1.14	2.70	1.04	0.38	no
COPROB	0.07	1.30	0.32	0.00	3.14	0.03	✓
EUOEUR	0.27	0.00	0.68	1.30	2.15	0.10	no

Subsequent analyses used only the November seedling data because the most recent seedling census was thought to most reliably represent the actual seedling population.

Consideration of data from only one census period was thought to be the most relaible method of integrating seasonal data in this instance particularly given the the non-significant differences between census periods (Table 5.2).

A Duncan's Multiple Range Test was performed on the November seedling census data. No significant difference in seedling density was observed between the four habitat types (Table 5.6), which is contrary to the result presented in Table 5.5. A similarly contrary result was produced for several species. Table 5.6 indicates no significant difference in seedling density for *Melicytus ramiflorus, Coprosma rotundifolia,* and *C. robusta,* and the Duncan's Multiple Range test indicated a significant difference between habitat types for *Coprosma virescens* and *Euonymus europaeus, contra* Table 5.5. Those significant differences which were observed generally separated scrub and forest types (e.g. for *Coprosma virescens*), indicating a possible relationship between species-level seedling density and successional stage.

Table 5.6. Duncan's Multiple Range test for November seedling census data; all species and 10 most abundant seedling species. Habitat types with the same letter are not significantly different at the 95% level.

SPECIES	S1	S2	F1	F2
ALL SPECIES	A	A	A	A
PARSPP	B	AB	A	B
CYTSCO	A	B	B	B
MELRAM	A	A	A	A
COPROT	A	A	A	A
MUEAUS	A	B	B	B
PITTEN	B	B	B	A
HOHSPP	A	A	A	A
COPVIR	B	B	A	AB
COPROB	A	A	A	A
EUOEUR	B	B	AB	A

ii. Ordination

The individual seedling counts at each site for the November quadrat census were used as the basis for a DCA ordination and the scatter plot produced by plotting the first two ordination axis scores is presented in Figure 5.2. Figure 5.2 presents a typically diffuse ordination scatter plot, with each of the four habitat types occupying a similar proportion of ordination space as they do in the initial vegetation ordination of Chapter 3 (Figure

3.1) Twice as much variation is accounted for in the first axis as in the second, and no gradient was longer than 4 s.d., indicating that complete species turnover did not occur (Table 5.7).

Table 5.7 Summary of DCA ordination of November census seedling counts.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.741	0.316	0.201	0.137
Gradient length	3.533	2.656	2.467	2.575
Cum. % variance	18.3	26.0	31.0	34.4

The individual species scores are plotted as Figure 5.3, and Table 5.8 lists the correlation coefficients for correlations between individual seedling species score at each of the 80 sites and DCA ordination axis position.

Table 5.8 Pearson product moment correlation coefficients (r) for correlation between per-species seedling counts and site DCA ordination axis position for each of 80 seedling count sites. Only $|r| > 0.25$ tabled.

AXIS 1		AXIS 2	
SAMNIG	-0.33	MELRAM	-0.42
COPCRA	-0.33	CYTSCO	-0.34
COPVIR	-0.32	COPROT	-0.27
PITTEN	-0.30	GRILIT	0.27
RUBSPP	0.31	HOHSPP	0.28
MELRAM	0.41	SOLLAC	0.28
		MEUAUS	0.29
		COPVIR	0.30
		EUOEUR	0.34

Clear trends are not apparent from the correlations presented in Table 5.8. The strongest correlations (both positive and negative) between Axis 1 position and seedling count are all for species typical of the forest habitat types, and Axis 2 correlations are very similar for mahoe and broom, which as described in Chapter 3 are the two species used to separate the scrub and forest types in the TWINSPAN analysis.

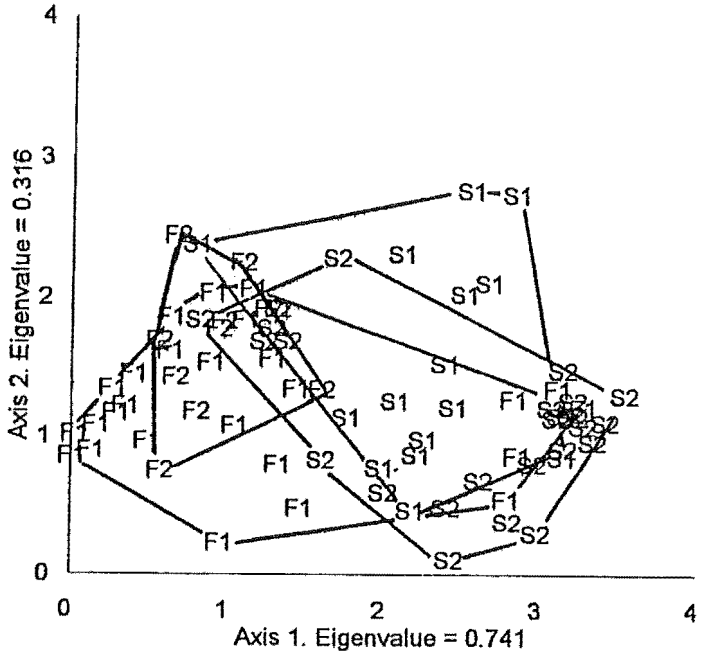

Figure 5.2. Scatter plot of DCA ordination site scores. November seedling survey data

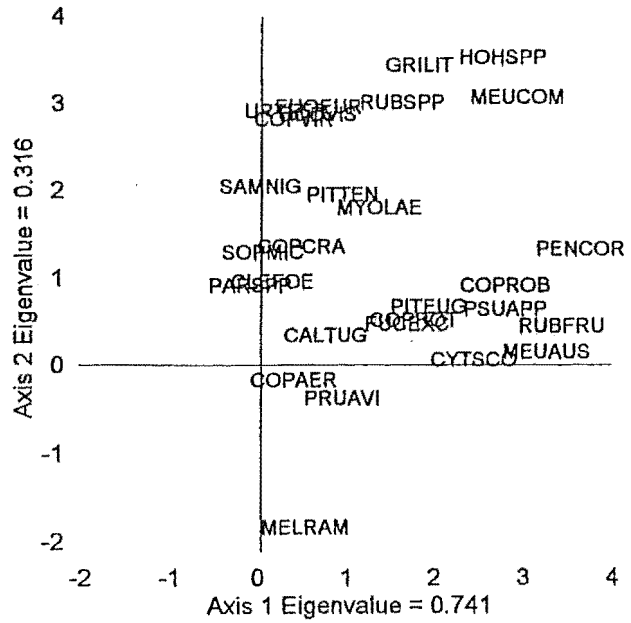

Figure 5.3. Scatter plot of DCA ordination species scores. November seedling survey data.

To assess the way in which seedling patterns are responding to vegetation on a per-species basis, coefficients of correlation were calculated between seedling counts for the November census and vegetation score at each of the 80 sites for each of the ten most abundant seedling species (Table 5.9). Table 5.9 presents some interesting results. The species which exhibit no or very weak relationship between vegetation score and seedling numbers ($|r| < 0.2$) are all bird dispersed species, and three of the species with $|r| > 0.2$ rely on abiotic dispersal, indicating a potential dispersal mediated response. This however is apparently confounded by the fact that the strongest observed relationship ($r = 0.58$) is for *Coprosma rotundifolia* which is a common understory species reliant on bird dispersal. Williams and Karl (1996) observed that *C. rotundifolia* was not commonly consumed by dispersing birds, which would explain at least in part the apparent lack of dispersal of this species. None of the correlations are strongly negative, indicating that the most abundant seedling species are either positively related to the presence of conspecific vegetation, or that there is no relationship between conspecific seedlings and vegetation.

Table 5.9 Pearson product moment correlation coefficients (r) between seedling counts and vegetation score at each of the 80 sites for the 10 most abundant seedling species.

SPECIES	r
PARSPP	0.36
CYTSCO	0.40
MELRAM	-0.05
COPROT	0.58
MUEAUS	-0.07
PITTEN	0.11
HOHSPP	0.46
COPVIR	-0.04
COPROB	0.28
EUOEUR	-0.03

iii. Seedling Diversity

The seedling-species diversity of each of the 80 quadrats was estimated using the Shannon Weiner diversity index, defined in Chapter 3. As with seedling density there was no difference in seedling-species diversity between census for all the quadrats ($F = 2.40$,

p = 0.09), although there were significant differences in diversity between the four vegetation types at all three census periods (Table 5.10).

Table 5.10. Mean seedling diversity as estimated by Shannen-Weiner index for each vegetation type at each measurement period.

	S1	S2	F1	F2	F	p	Sig.?
FEB.	0.554	0.633	0.864	0.642	11.24	0.00	✓
JUN.	0.439	0.651	0.926	0.853	11.15	0.00	✓
NOV.	0.635	0.692	1.102	1.165	8.651	0.00	✓
Duncans[1]	B	AB	A	A			

[1] Habitat types with the same letter are not significantly different at 95% level

A Duncan's Multiple Range Test indicated an apparent relationship between seedling diversity and successional stage, as the two most mature habitat types (F1 and F2) had significantly greater seedling diversity than the youngest habitat type (S1) (Table 5.10).

3. Summary

Periodic census of Hoon Hay Valley seedling populations indicated an apparently strong seasonal trend (Figure 5.1), although this trend was not statistically significant at either the overall level or at the level of the four habitat types (Table 5.2). Significant seasonal trends in seedling density were however observed for two of the ten most abundant seedling species, and high p-values associated with the other eight indicate that lack of observed significant difference may be more due to high variability in seedling density than any real trend (Table 5.3). There were significant between-habitat type differences in seedling density (Tables 5.5, 5.6) and diversity (Table 5.10), often indicating an apparent relationship with presumed successional stage.

3. DISCUSSION

a. Sources of bias

Because of the simple experimental design the only likely source of error is observer bias in identification of seedling species. Particularly when small, seedlings are difficult to identify to species as many species have similar morphologies at a very small size. It is likely that some seedlings were mis-identified on this basis, particularly for morphologically similar species such as the small- leafed shrubby species (*Coprosma* spp., juvenile *Hoheria* spp. etc.). This may in part explain the observed lack of significance of apparently strong seasonal density trends, although with increased

observer experience this source of error decreased and so it is unlikely that this observer bias is sufficiently strong as to weaken the integrity of the results presented above.

b. General Discussion

The overall seedling density of the 31 species observed ranged from a low of 1353 seedlings in June (17 seedlings m^{-2}) to a maximum of 2751 (34 seedlings m^{-2}) in the November census. Seedling densities for each of the species ranged from 0.0125 seedling m^{-2} for species with only one seedling observed to 16 seedlings m^{-2} for the most abundant species (*Parsonsia* spp). There were apparently strong inter-seasonal trends (Table 5.1 and Figure 5.1) although except for mahoe and *Parsonsia* these were not significant (Table 5.2 and 5.3). Seedling populations exhibited high variability, both spatially and temporally, leading to non-significant differences between habitat types for most of the ten most abundant species. These were commonly associated with high *p*-values, indicating that data variability was obscuring apparently significant trends.

There have been several studies in New Zealand forests which have investigated seedling density either directly, or as part of larger studies. These investigations tend to have been undertaken in mature forest and concerned only with an individual species of particular interest. For example in his seminal summary of beech (*Nothofagus*) ecology Wardle (1984) presents a summary of several investigations (e.g. Manson and Guest 1975; Wardle and Guest, 1977; Wardle 1970) of beech seedling dynamics where seedling densities ranged from ca. 0.05 seedlings m^{-2} to greater than 1.5 seedlings m^{-2}. In a more detailed study June and Ogden (1975) report seedling densities for red beech (*N. fusca*) ranging from less than 0.1 to up to ca. 8 seedlings m^{-2}, with wide differences between individual microsites. Other authors (Ogden *et al.*., 1987) report seedling densities range for single species from 0.02 to 0.2 seedling m^{-2}, and Norton (1991) reports seedling densities for four podocarp species in a west coast forest ranging from 0.18 seedlings m^{-2} for rimu (*Dacrydium cupressinum*) to over 1.3 seedlings m^{-2} for miro (*Prumnopitys ferruginea*), to give a total for the four species of ca. 2.5 seedlings m^{-2}.

Seedling density has also been reported from international studies. In a Japanese temperate deciduous forest Shibata and Nakashizuka (1995) report seedling densities for four co-occurring species of *Carpinus*, which average ca. 0.04 seedlings m^{-2}, although the range varied significantly with season and year, ranging from less than 0.005 seedlings m^{-2} in the autumn of the lowest year, to in excess of 0.52 seedlings m^{-2} in the spring of the most abundant year. Debussche and Isenmann (1994) report seedling densities in a patchy Mediterranean scrub ranging from 0.06 to in excess of 60 seedlings m^{-2}, with density related to significant influences of vegetation structural complexity with the greatest numbers of seedlings occurring in the most structurally complex vegetation.

Seedling densities in open sites with very low structural complexity were orders of magnitude lower than under closed canopy with greater structural complexity.

The seedling densities reported in the literature span several orders of magnitude, with numbers dependant on vegetation type, the species investigated, and the particular regeneration ecology of the vegetation investigated, and it is apparent that there is a wide spatial variability in seedling density both at the community level (e.g. Norton 1991, Wardle 1984, Debussche and Isenmann, 1994) and at the level of individual species (Shibata and Nakshuzika, 1995, Augspurger 1984, Wardle 1984). The seedling densities observed in the current study apparently high compared with these studies. This is probably related to the different vegetation types of the investigation, as most of the published studies are for forest vegetation, and only interested in one or a few individual species. The density range of Debussche and Isenmann (1994) in similarly scrubby vegetation indicates that the density observed in Hoon Hay Valley is within the range of published studies.

There was high spatial variability in seedling density, both overall and for the 10 most abundant species, and diversity of seedling populations, as indicated by significant differences in seedling density between the four habitat types in Table 5.4 and 55. Seedling density also varied widely at the quadrat-level, as indicated by the wide standard deviations observed in Tables 5.2 to 5.6. The reasons for this high variability are not immediately clear, and so several conceptual approaches to the explanation of spatial seedling distributions are considered, beginning with the Safe Site concept (Harper *et al.*, 1965).

The germination and recruitment of seedling populations is a multi-step process, and requires several things. Originally described by Harper *et al.* (1965) the Safe Site concept describes those features of a site necessary for the germination and establishment of seedlings. It requires the presence of certain factors - provision of the stimuli needed for the breaking of seed dormancy (temperature, light, moisture etc.), the conditions required for the germination processes to proceed (adequate moisture and light resources), the resources required in the course of germination, and the absence of hazards, such as predators, pathogens, and other generally detrimental factors (Harper, 1977).

The presence or absence of safe sites is operable at the very fine scale of an individual seeds, and at this scale the environment is extremely heterogeneous Harper (1977). Favourable conditions can be distributed at an exceedingly fine scale, particularly in terms of the factors necessary for the breaking of soil dormancy (moisture, light, temperature). Harper *et al.* (1965) observed that small changes in water tension and

resource availability associated with soil microtopography often had a large impact on seed germination rates. For instance Sheldon (1974) reported effects of the interaction of substrate microtopography and seed morphology on the germination of seeds of *Taraxacum officinale* on a water-supplying substrate. Seed germination varied widely dependant on the orientation of seed (above/below the surface, vertical/horizontal, upside down, etc.) (Sheldon (1974)). The heterogeneity of substrate/seed interaction operates at a spatial scale too fine to be of meaningful use in terms of large scale population investigation, although Harper (1977) states that it is important to think about developing plant populations in these terms and at the scale of environmental heterogeneity relevant to the individual seeds lest "the real events that make for life or death of the individual become lost in the statistics of vegetation, and real causes become lost in generalisations about correlations." (p. 112-113).

In a general way consideration of Safe Sites is dependant on factors affecting seed germination. Several authors have investigated the germination requirements of the seeds of native woody plant species in New Zealand. Fountain and Outred (1991) provide a literature review of some of the germination requirements of 113 native New Zealand vascular plants. They observed that little research has been published detailing the specific germination requirements (light regimes, temperature controls, hormonal inhibitors etc.) of many of the species they discuss, and so there is little that can be concluded in respect of these factors for the safe site requirements of many of the seed species observed in this study which would be of use in discussing the spatial distribution of seedlings observed.

However the most valuable insights currently available to the germination requirements of New Zealand native species are provided in several accounts by C.J. Burrows. As part of on-going work investigating the dispersal ecology of fleshy fruited native New Zealand woody species Burrows has published the results of investigations into the germination requirements of a suite of species, 27 of which were encountered in Hoon Hay Valley. Seeds were all subjected to a standard treatment (seeds cleaned, moist, well lit in an unheated glasshouse) and Burrows' observations are summarised in Table 5.11.

For all species with fleshy fruit germination was significantly retarded if parental tissues were not removed, indicating that fleshy tissues contain germination inhibitors. Removal of these, for example by passage through a frugivore's gut (see Chapter 4) is apparently required before germination can proceed. Other authors have observed that seeds contain germination inhibitors independent of fleshy parental tissue. Partridge and Wilson (1990) observed that mahoe seeds exude a brown water soluble substance which apparently acts as a germination inhibitor. They observed that mahoe seeds would not germinate until all the exudate was removed, and germination of pre-leached seeds was inhibited by

application of the exudate. The authors suggest that it confers an advantage on mahoe seeds by only allowing germination after periods of rain (but *c.f.* Clout and Tilley 1992).

Table 5.11. Summary of germination requirements of 27 species encountered in Hoon Hay Valley. Data from published work of C.J. Burrows.

SPECIES	SOURCE	NOTES
Fucshia excorticata *Grisilinea littoralis* *Melicytis ramiflorus*	Burrows 1995a	Bird dispersed Rapid and successful late summer/early autumn germination in light once fleshy parental tissues removed
Aristotelia serrata *Coprosma robusta* *Schlefflera digitata* *Cordyline australis*	Burrows 1995b	Rapid and successful germination once parental tissue removed. (summer/autumn) *Cordyline* only germinates as successfully in the dark as in the light. Small proportion of *Aristotelia* and *Cordyline* seeds over-wintered and germinated in following spring
Dodonea viscosa *Pennantia corymbosa* *Pseudowintera colorata*	Burrows 1995c	Germination of *Dodonea* slow and spans several seasons Main flush of *Pennantia* germination in spring. *Pseudowintera* begins germination in winter, and stops in summer.
Calystegia tuguriorum *Clematis foetida* *Mueuhlenbeckia australis* *Parsonsia heterophylla* *Rubus cissoides*	Burrows 1996b	Vines. Some *Mueuhlenbeckia* germinated in Autumn, most did not until following spring. Clematis did not begin germination until late winter, but all viable seeds germinated within 2 months. Germination of *Rubus*, *Parsonsia*, and *Calystegia* prolonged - seeds still germinating after 5 years.
Melicope simplex *Myoporum laetum* *Urtica ferox*	Burrows 1996c	*Myoporum* unusual - disseminule = four seeds enclosed in a fleshy endocarp. Germination slow - first germination after 1 month (*Urtica*), 5 months (*Myoporum*) or 7 months (*Melicope*). Germination continued up to 5 years. These species exhibit uncommonly deep dormancy. maybe a risk spreading strategy?

Pittosporum tenuifolium *P. eugenoides* *Plagianthus regius* *Psuedopanax arboreus*	Burrows 1996d	Germination in well lit conditions very high (>90%). All species germinated within 1 year. All germinated in dark, but success lower. Versatile germination behaviour matches both colonising and forest dwelling habit.
Alectryon excelsus *Kunzea ericoides*	Burrows 1996e	Germination <50% for *Alectryon*, but >90% in *Kunzea*. Buried seeds of *Alectryon* germinated well, buried *Kunzea* germinated poorly.
Hoheria angustifolia *Myrsine australis*	Burrows 1996f	*Hoheria* germinated well in the dark, *Myrsine* less so. *Myrsine* tolerated desiccation and germinated after burial, *Hoheria* did not. *Myrsine* has good seed bank potential.
Solanum lacinatum	Burrows 1996g	Germinates well in dark, survives burial well. High percent germination.

Several species in Table 5.7 have the potential to form part of a buried seed bank (e.g. *Parsonsia, Myoporum, Melicope*), and some exhibit dormancy several seasons or even years. Some species (e.g. *Hoheria*) will germinate in the dark, indicating that they have potential for germination beneath thick forest canopy, whereas the germination behaviour of others indicates that they are best suited to a colonising habit (e.g. *Plagianthus*). Burrows observed that most species listed in Table 5.7 germinated well in ideal conditions (moist, not buried, suitable light), indicating that factors other than inherent dormancy or germination inhibitors would be required to prevent germination if suitable Safe Site conditions were experienced. Some species (e.g. *Alectyron*) had apparently poor germination, although it is interesting to note that the germination success of *Alectryon* was apparently unaffected by 5 months of desiccation (Burrows 1996e). Some species apparently required over-winter stratification for germination (e.g. *Clematis*), and other authors have noted a stratification requirement for some of Table 5.11 species (see for example Moore *et al.* (1994) who observed a stratification requirement for germination of *Pittosporum*).

All these studies indicate that for the species encountered in Hoon Hay Valley germination is generally high provided that a few simple conditions are met. It follows from this that spatial patterns in seed germination are related to spatial expression of these simple Safe Site germination conditions. The observation that there are significant differences in seedling density between the habitat types (Table 5.4) indicates that there are likely to be significant differences in those environmental variables that are controlling germination.

Other authors have indicated the importance of microclimatic variables in the ecology of seed germination and establishment (e.g. Bazazz 1979, Hartgerink and Bazazz 1984, Taiz and Zeiger 1991), particularly light (Baars and Kelly 1996, Williams and Buxton 1989, Roxburgh 1992). Environmental variables were not directly assessed in this study so it is difficult to address directly the way in which environmental variables are determining spatial seedling patterns. Cullen (1996) provides a few useful insights into microclimatic variability in Hoon Hay Valley, and notes that microclimates in scrubby successional vegetation tend to be drier, warmer, and experience higher daily irradiance that those in more established forest. This would tend to indicate that germination would be higher in scrubby vegetation than in forest based on temperature and light requirements, although lower in terms of moisture requirements. Inspection of Table 5.4 indicates that there are significant differences in seedling density between the four habitat types assessed, indicating that the spatial distribution of Safe Sites in Hoon Hay Valley is related to habitat type. However the relative seedling densities of each of the habitat types of Table 5.4 is not constant for each of the census periods; for example seedling density is very similar in F1 and S2 in February, but in November F1 has a much higher seedling density than S2. This indicates either that the expression of safe site conditions for germination and establishment is not constant for the habitat types between seasons, or that factors other than this are determining spatial seedling pattern.

In any case, mere identification of factors necessary for a site to be 'safe' does little for explaining spatial patterns of seedling recruitment. One can identify those physical factors which are necessary to break dormancy, initiate and sustain germination and to maintain a growing seedling, but actual identification of safe sites in the field is effectively impossible. As stated the presence or absence of a safe site operates at the scale of an individual seed, so the only way to determine if a site is safe is if a seedling will germinate there (Harper, 1977). This is emphasised by Fowler (1988), who observed that the strongest influence on the probability of a seedling establishing at a particular site was the occurrence of an individual of that species there already. This is counter-intuitive when considering the potential benefits available to plants from dispersal discussed in Chapter 4. Fowler (1988) noted that safe sites are continuous rather than discrete phenomena - sites have degrees of 'safe-ness' which are reflected in probabilities of survival and seedling growth rates etc., and the 'safe-ness' of a site may vary temporally with a resolution similar to their fine-scale spatial resolution.

It is apparent then that there are factors other than germination and proximate safe site requirements determining the spatial seedling patterns observed in Hoon Hay Valley, and that post-germination factors are playing a part in spatial patterns as well. This is supported by Gill and Marks (1991) who found that in old field successions in central

New York post-germination factors were the most significant determinants of seedling pattern. An insight into the influence of post-germination factors on spatial seedling distribution is provided by consideration of the Escape Hypotheses derived as a result of studies investigating possible seedling-level causes of tree spacing in species-rich tropical forests.

The Escape Hypothesis (Howe and Smallwood, 1982) arises from the observation that seedlings enjoy increased fitness (survivorship, growth rates etc.) with increasing distance from their parent tree. It originates in the independent work of Janzen (1970) and Connell (1971) who suggested that because of the interactions of distance and density dependant mortality close to a parent tree, declining seed dispersal density with increasing distance form a parent, and increased probability of seedling survival with increasing distance, maximum seedling survival and recruitment would occur at some intermediate distance from the parent. Connell (1971) predicted higher progeny mortality close to a parent crowns because of the action of herbivores which normally feed on adults, and Janzen (1970) predicted that in addition to these distance responsive factors density responsive predators or pathogens would concentrate their activities near parent trees where the density of seed and seedlings would be highest.

However Hubbell (1980) points out that unless density dependant mortality is 100% adjacent to the parent tree seedling recruitment will still be greatest at close to the parent. He suggests that as seed dispersal declines exponentially with distance from the parent, even mortality approaching 100% will still result in seedling densities highest closest to the parent, as this is where most of the seeds are deposited; 5% survival of 10 000 seeds immediately adjacent to a parent will produce higher seedling densities than 50% survival of 100 seeds some distance away.

The Escape Hypothesis has become an important concept in explaining spatial patterns of seedling survival. Clark and Clark (1984) provide a substantial review of the evidence for the so-called Janzen-Connell model, and conclude in general that a "review of 24 data sets...showed that most evidence indicates either density dependence or distance dependence in progeny mortality, as hypothesised by Janzen and Connell." (Clark and Clark, 1984; p. 787). Even a cursory inspection of the seedling recruitment literature provides evidence supporting the acceptance of the Janzen-Connell Escape Hypothesis by Clark and Clark (1984). For example Augspurger (1984) reported decreasing mortality of seedlings of *Platypodium elegans* resulting from fungal pathogens with increasing distance. Howe *et al.* (1985) reported 99.2% seed mortality in seeds of *Virola surinamensis* between fruit drop and up to 12 weeks after germination, with seeds up to 45 m away from the parent tree experiencing a 44 fold advantage over seeds under parental canopies.

Evidence in favour of the Escape Hypothesis is not confined to tropical systems. In a study of seedling dynamics in an east Texas floodplain forest Streng *et al.* (1989) observed that the most important variable influencing seedling survival was distance to the nearest con-specific adult. Curiously this pattern was not due factors consistent with the Janzen-Connell model such as differential herbivory or pathogen activity, nor was it related to light or density dependant competition, as none of these factors showed a relationship with con-specific adult distance. The authors were unable to identify the factor which was causing the distance dependant seedling survival, and concluded that "the cause of low seedling survival near adult conspecifics...is unknown" (Streng *et al.* 1989, p 191).

The observations of increasing survival with increasing distance from the parent have been explained in terms other than those relating to parental proximity. Augspurger (1984) describes patterns of seedling recruitment in terms of a Colonisation Hypothesis whereby increased dispersal distance from a parent increases the chance that offspring will encounter a suitable establishment site. The Colonisation and Escape hypotheses are not mutually exclusive (Platt 1975), although the relative importance of each will vary depending the behaviour and germination requirements of the individual species, and the heterogeneity of the environment which the species are occupying (Augspurger 1984, Hartgerink and Bazazz 1984).

The Escape and Colonisation hypotheses are in part testable for Hoon Hay Valley with data presented in Table 5.9, which presents correlations between seedling density and vegetation scores for the ten most abundant seedling species. For the Escape and Colonisation hypotheses to be true for the Hoon Hay Valley data, species correlations would have to be significant and negative; both hypotheses indicate that seedling survival and recruitment will be highest away from con-specific adult plants and hence seedling survival should be inversely proportional to vegetation score for each species. Inspection of the results presented in Table 5.9 indicates that this is not the case. Correlation coefficients are either close to zero indicating no relationship between seedling and con-specific vegetation cover, or positive, indicating that seedlings are positively associated with con-specific vegetation. The data presented in Table 5.9 show that seedlings are not negatively associated with parental proximity, indicating that neither the Escape or Colonisation hypotheses are valid for the data presented.

Confident refutation of the Escape and Colonisation hypotheses based on data presented in Table 5.9 rests on the assumption that the data allows these hypotheses to be tested, but because of the way in which data has been collected this may not be the case. Seedling data is derived from randomly located quadrats, and vegetation data is derived

from unbounded 5 m radius survey plots. While these rely on the same 30 m spaced transect stations as a base, the spatial relationship between each of the quadrats and vegetation survey points is random. Testing of the Escape and Colonisation hypotheses relies on defined distance relationships, but because of the random nature of the quadrat and vegetation survey point placement these cannot be definitely enumerated. Because of this, rejection of the Escape and Colonisation hypotheses should be taken on an indicative level only.

The refutation of the Escape and Colonisation hypotheses for Hoon Hay Valley is apparently confounding, particularly given the weight accorded to the Escape hypothesis in the ecological literature. Some solace can be however be taken as recent literature indicates that factors associated with parental-distance and density dependant recruitment are not straightforward. For example Willson *et al.* (1987) report results from an experimental manipulation of sibling density in *Phytolacca americana* in which no evidence for density dependant competition was observed. It was even suggested that siblings growing together may do better, at least temporarily, than seedlings growing with conspecific non-siblings. This observation is supported for recruitment of two co-occurring grasses in a Texas grassland; both *Aristida longiseta* and *Bouteloua rigidiseta* had higher probabilities of survival from germination and grew larger in the early stages of growth if they had one or more seedlings or juvenile plants of either species within 2 cm of them (Fowler 1988). This implies that competition with other seedlings either did not occur, or was so weak that it was overridden by other factors. Augspurger and Kitajima (1992) produce results which put another twist on the density dependant Escape Hypothesis. In an experimental study of seedling recruitment of *Tachigalia versicolor*, a wind dispersed species on Barro Colorado Island, it was observed that at a large spatial scale (defined as a 100 m radius from the parent) high seedling density increased seedling survival as a result of predator satiation. Seedling recruitment was greatest where the density of seedlings was greatest (again <100 m from the parent) "greatly exceeded" recruitment up to the limit of seed dispersal (assessed up to 1800 m), and even at the smallest spatial scale (< 1 m) density dependant effects appeared to play only a minor role in explaining spatial patterns of seedling recruitment.

Assuming that the Escape and Colonisation hypotheses can be validly rejected for the Hoon Hay Valley data it is apparent there are factors other than distance and density dependant factors which are determining the spatial pattern of seedling germination and recruitment.

Spatial seedling pattern is determined by what can be thought of as a series of filters. As described in Chapter 4 there are significant spatial patterns in seed rain, with these related to factors such as vegetation structure and disperser behaviour. As establishment

of seedlings is dependant on a source of seed many of the factors giving rise to spatial pattern in seed rain will be similarly responsible for spatial pattern in seedlings, and this can be thought of as the first spatial filter. Germination and survival of these seeds is then determined by the second spatial filter; factors operating at the scale of an individual seed best described in terms of the safe site concept of Harper (1977). It is apparent from Burrows' observations that most of the seeds likely to be encountered in Hoon Hay Valley seed rain have quite high rates of germination once several simple conditions are met (even if this germination spans several seasons (Table 5.11)), and so spatial seedling patterns will be also governed by spatial distribution of suitable safe-sites. Post-germination factors such as predation and environment-mediated mortality will be acting as the final filter on seedling survival.

It is clear that the observed spatial pattern of seedling distribution is dependant on many factors, most of which were not directly observed in this study. As will be shown in the following Chapter factors associated with seedling germination and establishment can have significant implications for processes of vegetation change. On the basis of this factors determining the spatial pattern of seedling populations in Hoon Hay Valley are most certainly deserving of further investigation.

CHAPTER 6

SYNTHESIS

1. INTRODUCTION

The preceding Chapters have provided the base information for the synthesis that is contained within this Chapter. As described in the Introduction (Chapter 1) the overall aim of this thesis is to investigate the multi-step process of seedling recruitment operating in Hoon Hay Valley. Seed dispersal and seedling recruitment are keystone ecological processes, as the factors operating at this stage in the population recruitment cycle have potentially the largest effects on future population and community composition and pattern (Harper 1977, Herrera *et al.* 1994). The potential ecological and evolutionary significance of plant dispersal traits will depend on the degree of coupling between pattern of seed dispersal, seed rain, and subsequent demographic processes operating at the seedling stage (Harper 1977).

As described by Herrera *et al* (1994) investigation of coupling between patterns of vegetation, seed rain, and seedling populations yields insights into processes of vegetation change. Tight coupling of each stage of the conceptual recruitment pathway indicates that vegetation is changing little as there is no difference in patterns between each of the conceptual steps. Alternatively if each stage if loosely coupled then vegetation is changing, as each step is only loosely related to the one previous. Assessment of nature and extent of inter-step coupling provides a direct measure of vegetation change.

2. METHOD

The data presented in the previous three chapters represents a complex multi-dimensional data set presenting data on steps along the conceptual recruitment pathway which have been investigated in this study. Chapter 3 presents data on the structure, composition, and distribution of the vegetation communities present in the Valley, Chapter 4 presents detailed information on the spatial and temporal patterns of seed rain that were observed in the Valley during the measurement period, and Chapter 5 presents the results of censuses of seedling populations which are present. In order to enumerate the degree of coupling between them, these datasets must somehow be compared. What is required is a method for simply and comprehensibly comparing complex datasets of

spatially related data. It is apparent that there is a very large number of possible comparisons as each site has data for seed rain, vegetation composition, and seedling census. This data is available for each species present and over several time periods. A simple method of firstly summarising this data, and secondly comparing these summarised data sets is required.

As described in Chapter 3 ordination techniques offer a method of summarising individual site by species data. Ordination arranges sites/individuals along axes in a multi-dimension space based on their attribute data. The sites used in the investigations of vegetation structure, seed rain, and seedling recruitment in this study are spatially related, so a comparison of the relative position of each site in each of the derived ordination spaces will provide an indication of the degree and nature of the relationship between each step. In the theoretical situation where vegetation, seed rain, and seedling recruitment are perfectly coupled (i.e. all species are present at each stage in identical proportions) the relative position of plots/sites in ordination space of each of the three steps will be identical. Hence a comparison of ordinations produces a direct indication of the way in which each of vegetation, seed rain, and seedling recruitment are related.

There are several possible methods of comparing ordinations and Gower (1989) provides a review of these. Particularly noteworthy are techniques of Procrustes Analysis which have the general aim of deriving a transformation to fit the spatial distribution of points in one derived ordination space to the spatial distribution of points in another such that the residual sum of squares of the difference between the two sets of points in the combined ordination space is minimised (Gower 1989). These techniques would appear to offer potential for comparison of the ordinations presented previously. Procrustes techniques are however limited in that aside from detailing the 2 or 3 way matrix transformations associated with fitting ordination spaces of comparison the relationship between the ordinations is not quantitatively described nor it strength assessed; the result of Procrustes Analysis is a 2D ordination plot (Gower 1975, 1989) with the associated problems of subjective interpretation detailed in Chapter 3. To be of use in this study a defined relationship between ordinations of known strength is required.

Regression techniques are an obvious alternative. As in Procrustes analysis, regression is a least-squares technique in that a relationship is derived such that the difference between the observed and derived response variable is minimised (ter Braak and Looman 1987). In this instance at least, least-squares regression has the advantage over Procrustes analysis as it produces a predictive relationship (a regression equation) with a regression coefficient (R) giving a direct measure of the strength of the relationship derived.

The use of linear least squares regression offers a relatively simple technique for comparing ordinations. Firstly ordinations were derived for each of the datasets described in Chapters 3 through 5 using the technique of Detrended Correspondence Analysis (DCA) as detailed in Chapter 3. A correlation matrix was then derived for the first two axes of each ordination to indicate which axes which are most strongly describing the relationship between the ordinations. The position of each of the 80 sites on the ordination axes selected was then compared with least squares regression, with the relationship derived providing a direct measure of spatial coupling of each step on the conceptual recruitment continuum.

3. RESULTS

As described in Chapters 3 to 5, two-dimensional DCA ordinations were derived for species attribute data for each of vegetation, seed rain, and seedling spatial pattern. In order to select ordination axes for further investigation coefficients of correlation (in this case *r*, the Pearson product moment correlation coefficient) were calculated between the first two axes of each ordination (Table 6.1).

Table 6.1. Pearson product moment correlation coefficients (*r*) for DCA axis correlations. First two axes only.

		VEGETATION		SEED RAIN	
		Axis 1	Axis 2	Axis 1	Axis 2
SEED	Axis 1	0.50	0.26		
	Axis 2	**0.65**	0.20		
S'LING	Axis 1	**0.64**	-0.09	-0.09	**0.54**
	Axis 2	-0.14	0.22	-0.06	-0.03

The highest coefficient of correlation between each of the separate ordinations is marked in bold (Table 6.1) and these axes were then used as the basis of more detailed analysis; as they produce the strongest relationship they are most likely to be of use in illustrating the relationships of interest. The first axes of the vegetation and seedling ordinations offer the strongest correlations, whereas correlations are highest with the second axis of the seed rain ordination. The relationship between these axes was determined using least squares regression for both the overall relationship, and for individual habitat types.

a. Step 1. Vegetation - Seed Rain

The relationship between vegetation and seed rain ordinations is shown in Figure 6.1. The relationship is positive (seed rain = 0.39vegetation + 0.6), with a regression coefficient of $R^2 = 0.42$, indicating that spatial patterns of vegetation and seed rain are weakly coupled.

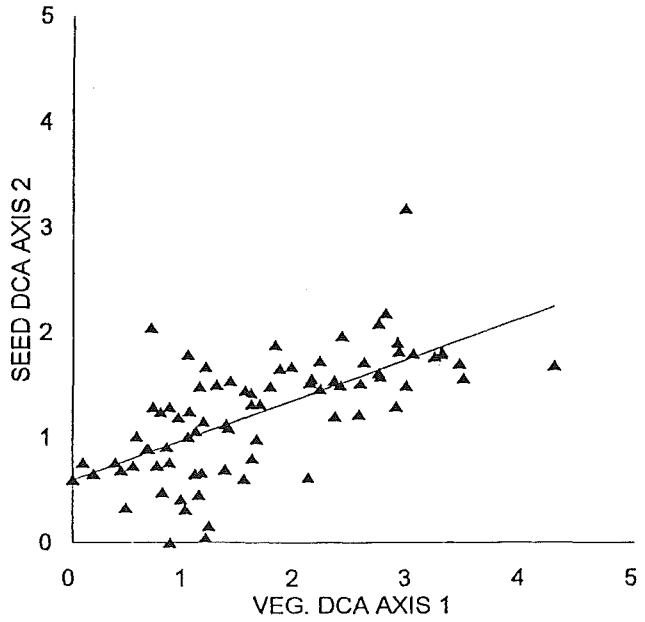

Figure 6.1 Relationship between vegetation and seed rain DCA ordination site scores.

However at the level of the individual habitat types the relationship between the vegetation and seed rain ordinations is different, in terms of both the nature and strength of the relationship (Table 6.2).

Table 6.2 Least squares regression equations and coefficients of correlation for comparison of 1st DCA axis of the Vegetation ordination with the 2nd axis of the Seed Rain ordination.

Habitat Type	Regression Equation	R^2
Overall	seed rain = 0.39 vegetation + 0.61	0.42
S1	seed rain = 0.18 vegetation + 1.30	0.08
S2	seed rain = 0.31 vegetation + 0.70	0.30
F1	seed rain = 0.41 vegetation + 0.62	0.21
F2	seed rain = -0.32 vegetation + 0.80	-0.09

Spatial patterns of vegetation and seed rain are least strongly coupled in the two habitat types with the least number of sites, suggesting that their low regression coefficients are more a reflection of sample size than and weakening of the overall relationship.

b. Step 2. Seed Rain to Seedlings

The relationship between the second seed rain DCA axis and the first seedling DCA ordination axis is also positive (Figure 6.2), with a regression equation of seedlings = 1.0 seed rain + 0.55 and a regression coefficient of $R^2 = 0.29$. Again the relationship is not constant between the habitat types (Table 6.3) with coefficients of correlation being so weak in the two smallest habitat types (F2 and S1) that there is effectively no relationship.

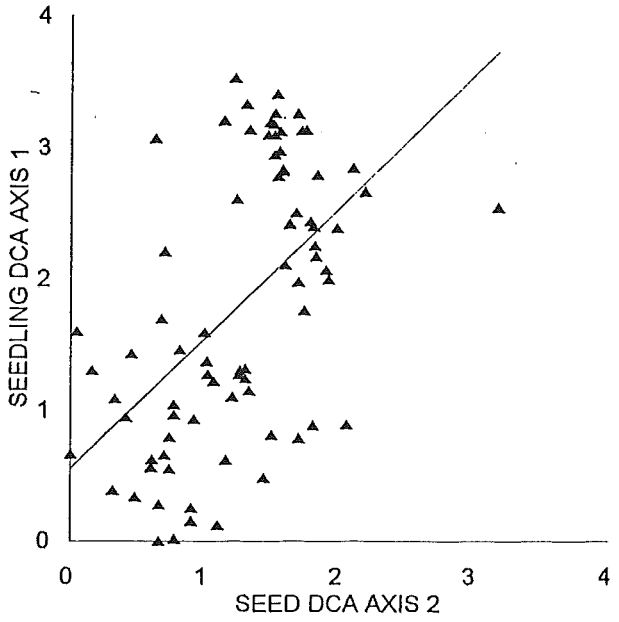

Figure 6.2 Relationship between seed rain and seedling DCA ordination site scores.

Table 6.3 Least squares regression equations and coefficients of correlation for comparison of 2nd DCA axis of Seed Rain ordination with 1st DCA axis of seedling ordination.

Habitat Type	Regression Equation	R^2
Overall	seedlings = 1.0 seed rain + 0.55	0.29
S1	seedlings = 0.18 seed rain + 1.94	0..03
S2	seedlings = 0.76 seed rain + 1.54	0.13
F1	seedlings = 1.16 seed rain - 0.14	0.35
F2	seedlings = -0.09 seed rain + 0.96	-0.01

c. Step 3. Vegetation to Seedlings

Step three examines the relationship between established vegetation patterns and the future vegetation pattern represented by the seedling population (Figure 6.3). Once more the relationship is positive, and the general relationship seedlings = 0.71vegetation + 0.61 with a regression coefficient of $R^2 = 0.41$.

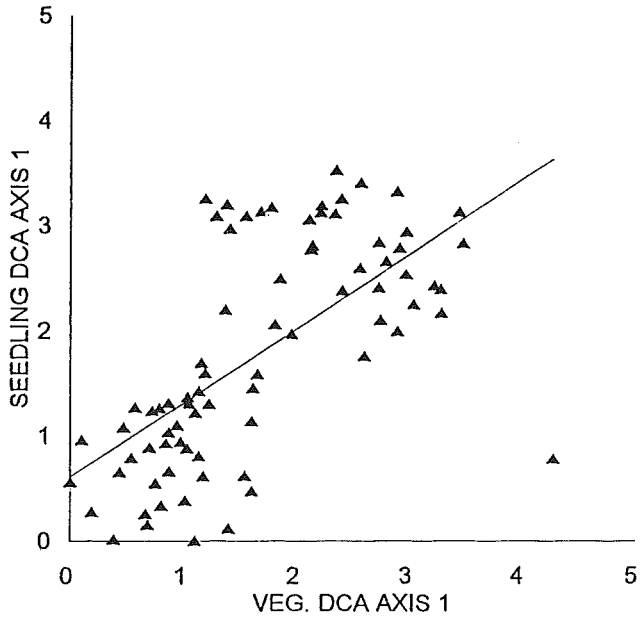

Figure 6.3 Relationship between vegetation and seedling DCA ordination site scores.

However examination of Figure 6.3 reveals the presence of a significant outlier at approximately (4,1), and removal of this significantly improves the strength and nature of the relationship to seedlings = 0.83vegetation + 0.45 with a regression correlation of $R^2 = 0.50$. Table 6.4 lists the relationships at each of the four types with the large outlier mentioned above removed.

Table 6.4 Least squares regression equations and coefficients of correlation for comparison of 1st DCA axis of Vegetation ordination with 1st DCA axis of seedling ordination (Outlier removed).

Habitat type	Regression Equation	R^2
Overall	seedlings = 0.83 vegetation + 0.45	0.50
S1	seedlings = 0.27 vegetation + 1.65	0.25
S2	seedlings = 0.63 vegetation + 1.27	0.41
F1	seedlings = 1.08 vegetation - 0.1	0.37
F2	seedlings = 0.46 vegetation + 0.63	0.24

It is apparent that there are large differences in the degree of coupling when each of the relationships is considered at the level of the four individual habitat types. The coupling indicated in Tables 6.4, 6.5, and 6.6 is always weakest in the habitat types with the fewest sites (F2 and S1) suggesting that these differences may be related to small sample sizes rather than a weakening in the overall relationship. Tables 6.4, 6.5, and 6.6 also show that the strongest relationship is always at the overall level (i.e. all 80 sites combined).

Between-habitat type differences may be due to floristic/compositional differences, as it is apparent that the relationships are different when viewed at the level of individual species. Table 6.7 lists coefficients of correlation for comparison of individual score (not ordination position, as in correlations just presented) for 10 common species (those listed in Table 4.4) which show that there are large species-level differences in the degree of continuity between each of the vegetation→seed rain→seedling steps. At times the individual species correlations are stronger than the overall ordination correlations presented in Tables 6.3 to 6.6, and at others the correlations are weaker. However the observation that the relationships is always strongest at the overall level rather than for any single habitat type indicates that it is at the habitat-type level that processes of vegetation change are being most strongly expressed.

Data presented in previous Chapters (notably Tables 4.4, 5.5., and 5.8) indicates that spatial patterns can be quite species dependant. Because of this, given the differences in species composition between habitat types, the weak coupling of spatial patterns at the habitat-type level shown in Tables 6.2, 6.3, and 6.4 is likely to have been mediated by species level relationships. Species-level coupling is shown in Table 6.5, which lists correlation coefficients for comparisons of individual species scores (i.e. vegetation scores, seed and seedling numbers rather than ordination axis position) for ten common Hoon Hay Valley species.

Table 6.5. Squared Pearson product moment correlation coefficients (r^2) for each of vegetation → seed rain → seedling for each of the species listed in Table 4.2.

SPECIES	VEG. V. SEED	SEED V SEEDL.	VEG. V SEEDL
MELRAM	0.03	0.04	-0.00
CLEFOE	0.06	0.03	-0.00
CYTSCO	0.56	0.13	0.16
ARISER	0.90	0.52	0.34
COPVIR	0.31	0.08	-0.00
PARSPP	0.42	0.35	0.13
HOHSPP	0.22	0.92	0.21
LEYFOR	-0.00	0.00	0.00
SAMNIG	0.14	-0.00	-0.03
DODVIS	0.79	-0.00	-0.00
MEUAUS	0.03	0.03	0.00

Individual species exhibit quite wide differences in the degree of coupling between each of the conceptual recruitment steps. For example mahoe (MELRAM) exhibits low coupling at all stages of recruitment, whereas *Hoheria* spp. (HOHSPP) has very high coupling between patterns of seed rain and seedlings. It is interesting to note that there is a dispersal-mode trend exhibited in Table 6.5, with species reliant on biotic dispersal apparently showing weaker coupling (i.e. stronger dispersal) than species dependant on abiotic dispersal (wind, gravity). This trend is summarised in Table 6.6, which shows the average correlation coefficient for each of the 11 species of Table 6.5, and compares these on the basis of dispersal mode. Mean coupling for biotic dispersed species was 0.14, whereas coupling for abiotic-dispersed species was 0.22. These differences were however not significant ($t = 1.07, p = 0.16$), probably a result of small sample size.

Table 6.6. Mean correlation coefficient for Table 6.5 species separated by dispersal mode. $t = 1.07, p = 0.16$.

BIOTIC		ABIOTIC	
MELRAM	0.035	CLEFOE	0.030
ARISER	0.587	CYTSCO	0.283
COPVIR	0.130	PARSPP	0.300
LEYFOR	0.000	HOHSPP	0.450
SAMNIG	0.057	DODVIS	0.263
MEUAUS	0.020		
Mean	**0.14**		**0.22**

c. Summary

The results presented in Tables 6.2, 6.3, and 6.4 indicate that there are continuities between the spatial patterns of vegetation, seed rain, and seedlings in Hoon Hay Valley. All the relationships are positive indicating that each step on the conceptual recruitment pathway is coupled to the previous step in a predictable relationship. These relationships are summarised in Table 6.7.

Table 6.7. Summary of regression relationships presented in Tables 6.2, 6.3, and 6.4.

	Regression	R^2
Vegetation → Seed-Rain	vegetation = 0.39 seed rain + 0.61	0.42
Seed-Rain → Seedlings	seed rain = 1.0 seedlings + 0.55	0.29
Vegetation → Seedlings	vegetation = 0.83 seedlings + 0.45	0.50

There is a large discontinuity between each of the steps on the conceptual recruitment continuum. Coupling is strongest at the vegetation→seedling stage (R^2 = 0.50), intermediate between vegetation and seed rain (R^2 = 0.42), and weakest at the seed rain →seedling stage (R^2 = 0.29). The largest discontinuities are associated with seed rain and germination, but the observation that the strongest correlation occurs between seedlings and vegetation indicates that these discontinuities are not translated directly to the vegetation→seedling stage. Coupling is always stronger at the overall level (i.e. all 80 sites combined) than at the level of the individual habitat types, indicating that within habitat-type processes of vegetation change are stronger than the processes of vegetation change at the overall level.

4. DISCUSSION

a. Sources Of Error

i. Methodology of overall study

The synthesis presented in this Chapter rests on data presented in Chapters 3 through 5, representing the stages on the conceptual recruitment pathway described in Chapter 1. Each of these Chapters has potential methodological weaknesses which are discussed in context, but each Chapter relies on the overall experimental design of which this Chapter represents the culmination. The most significant criticism that can be made of this study is that it is attempting to investigate spatial processes which are operating at a time scale

significantly greater than that available for the study, and so relies on summarisation and inference, both spatially and temporally.

ii. Spatial considerations - implications of scale.

Throughout this study data has been collected at a certain spatial scale on the unspoken assumption that the scale at which measurements are being made corresponds appropriately with the scale at which the processes of investigation are operating. This may not necessarily be a valid assumption. For example seed rain has been assessed on the basis of a semi-random array of seed traps placed between 20 and 40 m apart (5 m random placement using a 30 m transect spacing as the base), and it is possible that patterns of seed rain are best expressed at scales other than this.

It is true that observations of nature are a product of the way in which the observations are made. Indeed as Allen and Hoekstra (1991) say "the entities which emerge in a dataset are scaled by virtue of the observation protocol, and the filters applied to the dataset during analysis"; this scaling is not an intrinsic property of nature, rather it is a product of our observation and analysis. The problem arises then in matching the scale (both temporal and spatial) of our observation and analysis with the scale of heterogeneity in the 'real world', for any 'real world' phenomena will only become apparent if the scale at which they occur is matched by the scale of the observer/observation and any subsequent analysis (Allen and Hoekstra 1991, Kotliar and Wiens 1990). Allen and Hoekstra (1991) offer another cautionary note which relates to this and mention that natural process are essentially continuous inherently without boundaries. Patterns which emerge in nature should be thought of as a product of our observation of nature, rather than an intrinsic property of nature alone.

It follows from this that an explicit assumption of this study is that the scale at which observations have been made corresponds to the scale at which patterns and processes are occurring in the 'real world' of Hoon Hay Valley, and the inferences made on the basis of these observations are a truthful reflection of the material world. This may not be the case, and although it is difficult to assess it is possible that different results could have been obtained had a different sampling strategy been used.

However confidence can be expressed in the scale of sampling in the observation that at all levels of investigation significant spatial differences were observed. Between habitat-type differences were generally always significant, and this would not be the case had data been collected at an inappropriate scale.

iii Spatial considerations - autocorrelation and the weakness of classical statistics.

One of the tacit assumptions of this study is that there is an underlying spatial structure to the processes under investigation. For example consideration of the response of variables to differing habitat types in Chapters 3 through 5 assumes that there are (spatially distributed) differences between habitat types. In 'classical' statistics a fundamental assumption is that the individuals of interest in observation are independent, and if this assumption is not valid then the results derived from many inferential statistics are invalid (Ott and Mendenhall 1985). The existence of spatial structure implicitly refutes the validity of this assumption. If the nature of the spatial structure is known then one is able to predict to a greater or lesser extent the value of a second sample based on the value of the first sample; in the presence of spatial structure samples are not independent. In such situations data are said to be autocorrelated as it is possible to predict values at one point based on the observation of values at another (Fortin *et al.* 1989, Legendre and Fortin 1989, Legendre and Legendre 1989). Division of data into habitat types in this study is an explicit expression of spatial autocorrelation, as it is assumed that variability of observations obtained within a habitat type is less than the variability between habitat types. This is the hypothesis which is tested in analysis of variance (ANOVA) and the validity of this assumption is confirmed by the ANOVA between habitat-type differences in Chapters 4 and 5. Autocorrelation is also subject to the scale considerations mentioned above, as the scale at which observations are made influences the nature and magnitude of the autocorrelation. In the presence of a spatial gradient, observations at fine scale (relative to the scale at which the gradient is operating) will be positively correlated, whereas distal observations will tend to be negatively correlated (Cliff and Ord 1981).

iv. Spatial considerations - implications for this study

As has been stated the aim of this study is to assess the inter-linked processes of seedling recruitment in Hoon Hay Valley, and the data presented in Chapters 3 to 5 have been gathered in a manner which allows this to be achieved. All data has been gathered in an independently semi-random manner using the same 30 m spaced transect points as a base and because of this has a large inherent autocorrelation. However confidence in the results can be expressed quite strongly for the simple reason that the adverse effects of these scale dependant and auto-correlative factors are essentially dissipated in the summarisation of individual species data at the ordination stage, and so comparison of summarised ordination scores can continue without direct consideration of sub-optimal sampling at the level of the individual.

v. Temporal considerations

The time constraint of this study necessitated sampling of all the measured variables over periods shorter than ideal, and this has the potential to weaken the validity of any

conclusions drawn from the results presented. As described in Chapter 4, seed rain was sampled for a period of only 5 months (January to May) based on the results of previous studies in the same area (Burrows 1994a, 1994b). However once the seed counting was completed and the data collated in October/November it was apparent that this period had not sampled all the seed rain. The greatest seed rain was produced at the end of the measurement period and that seed rain, for two significant species at least, was still trending upwards. By this time it was too late to undertake further sampling as several seed traps had been dismantled and traps had not been cleared for several months. However investigation of Table 6.6 indicates that the species for which the short seed rain sampling affected were playing a subsidiary role in determining the seed rain ordinations. Even though mahoe formed one end of the second seed-rain DCA axis it is suggested that an incomplete seed rain sample would not have had a significant adverse effect on the overall spatial seed rain pattern and so does not significantly weaken the overall result. It is however acknowledged that the validity of this suggestion cannot be effectively tested.

b. General Discussion

i. Vegetation → Seed Rain

As indicated in Table 6.7 there is a positive association between spatial patterns of vegetation and seed rain. As described in Chapter 5 the majority of seed falls at only a short distance from the parent plant, and a positive coupling between patterns of vegetation and seed rain can be interpreted as being consistent with that observation. However the observed relationship is only weak ($R^2 = 0.42$), and this uncoupling of spatial pattern is most likely due to spatial patterns of seed dispersal as described in Chapter 5.

It should be remembered that the positive correlation between vegetation and seed rain of Table 6.7 is between spatial pattern as described by ordination axis position rather than data at the level of individual vegetation score or numbers of seeds. As indicated by Table 6.5 the correlations between vegetation scores and seed rain counts are highly variable at the level of the individual species, with some species exhibiting significantly higher coupling than others. Although the dispersal-trait comparison of Table 6.6 is not significant, species-level differences in dispersal traits are at least partly contributing to the uncoupling observed. Species reliant on biotic dispersal (e.g. *Melicytus ramiflorus*, *Leycesteria formosa*) generally have weaker coupling than those reliant on abiotic dispersal (e.g. *Dodonea viscosa*). This is particularly relevant when considering the between-habitat type differences is species composition. Some of the species with particularly high coupling (e.g. *Dodonea viscosa*, *Alectryon excelsus*) are highly habitat-

specific in their distribution whereas others with low coupling (most notably *Melicytus ramiflorus*) are not.

Dispersal mediated uncoupling is also introduced as a result of disperser behaviour. As described in Chapter 4, several studies (e.g. Norton 1991, Burrows 1994b, Howe 1986) have observed that bird dispersers will ingest seed in one tree and fly to another, commonly of a different species, for regurgitation or digestion/defecation. While disperser behaviour was not directly addressed in this study, the observation that fleshy-fruited bird dispersed species typically have lower coupling than species reliant on abiotic dispersal is consistent with the disperser mediated spatial patterns observed in other studies (Norton 1991, Burrows 1994b).

Another factor contributing to possible weakening of spatial correlations between vegetation and seed rain is the observation of several authors, notably Burrows (1994b), that con-specific individuals can exhibit large variability in fruit and seed production in a single growing season. While fruit production was not directly addressed in this study, variability in seed production at the species level indicated by Burrows and others will be in part contributing to discontinuities in spatial vegetation and seed rain patterns.

A further weakening in spatial coupling at the vegetation→seed rain stage may be introduced by dioecy. Several of the most abundant plant species present in the Valley are dioecious and commonly with a male-biased sex ratio (Godley 1964, Powlesland 1984). Given that most seed falls beneath a parent, it is less likely that a strong positive relationship would exist between seed rain and biomass for male plants of a dioecious species. The extent to which this has affected spatial coupling is unable to be assessed as the sex of the individual species was not assessed. Given that the most abundant vegetation and seed species (mahoe) is dioecious, the potential for dioecy to be influencing spatial coupling should not be overlooked.

ii. Seed Rain → Seedlings

Patterns of seed rain and seedlings are spatially coupled (Table 6.7), but as the relationship has the lowest regression coefficient of those presented in Table 6.7 (R^2 = 0.29) it represents the largest discontinuity along the conceptual recruitment pathway. Explanations for this discontinuity can be addressed in terms of factors already described in Chapters 4 and 5. It is apparent from those Chapters that there are significant spatial patterns of seed rain and seedling populations, and it is equally apparent from this Chapter that those patterns do not coincide.

Chapter 5 begins discussion of seedling spatial patterns by considering the Safe Site concept of Harper *et al.*. (1965). As described in Chapter 5 most of the species present in Hoon Hay Valley seed rain are apparently quite catholic in their germination requirements, and so one of the significant factors explaining seedling spatial patterns is the spatial patterns of those Safe Site environmental conditions to which seedlings are responding. Although safe sites were not directly assessed in this study it is highly likely that the observed between-habitat types differences in seedling pattern (and associated uncoupling of spatial pattern) are due at least in part to between habitat-type differences in safe site conditions.

It is also apparent from the Chapter 5 discussion that other post-germination factors are exerting significant influence on spatial patterns of seedling survival. As these were not directly assessed in this study definitive conclusions with respect to the factors likely to be significant in controlling post-germination seedling survival are difficult to make with the limited data presented in Chapter 5. A few factors are however able to be considered based on other research.

Discontinuities may be a result of differential mortality due to animal herbivory. As part of a study of mammal diet in Hoon Hay Valley undertaken concurrently with this study, O'Cain (1997) investigated the effects of mammal browsing on seedling populations with the use of animal exclosure plots. He observed that there was no significant difference between seedling populations inside the exclosure plots with those outside the plots, and that on the basis of this mammals were not having a detrimental effect on the overall seedling population. In spite of the lack of significant impact of browsing reported by O'Cain, it is suggested that animal browsing represents a substantial negative influence on seedling populations in Hoon Hay Valley, particularly when considering the at times spectacular increase in seedling numbers reported in studies where browsing animals have been removed. For example Allen *et al.* (1994) observed significant increases in seedling germination following eradication of Norway rats (*Rattus norwegicus*) from Breaksea Island, and this was explained partly in terms of reduced herbivory.

The increases in seedling numbers observed by Allen *et al.* (1994) may be due to reduced post-dispersal seed predation, rather then herbivory effects *per se*. Post dispersal seed mortality is definitely a contributing factor to the observed seed rain/seedling uncoupling (Houle 1992), although Burrows (1993) has suggested that the most significant source of post-dispersal seed death is likely to be soil micro-organisms (Burrows 1993).

Another possible cause of spatial discontinuity between seed rain and seedling populations is recruitment of seedlings from soil seed banks. Germination of seeds buried in soil seed banks has been the subject of much interest for regeneration of secondary vegetation (van der Valk and Pederson 1989, Alvarez-Buylla and García-Barrios 1991, Partridge 1992) as buried seeds are often the propagule source for initial colonisation following disturbance (Harper 1977, Grubb 1988, Luken 1990).

Seed bank recruitment was not directly assessed in this study. However Partridge (1989) investigated the soil seed banks of secondary vegetation on the Port Hills, including some sites within Hoon Hay Valley. He found that persistent deeply buried soil seed banks of gorse, broom, and less commonly kowhai were found at sites currently lacking these species in their vegetation, indicating that they had come from vegetation previously established at those sites. Forest sites tended to have more seeds from more species in their seed banks than sites with grass or scrub cover, and in general the soil seed bank in grassland sites was very similar in composition to the vegetation already present. Bracken dominated sites commonly had large persistent buried seed of gorse and broom, with a few seed species probably dispersed from adjacent forest patches. Similar trends were exhibited by scrub dominated sites, but forest sites typically had a large and complex soil seed bank, with seeds present from species present in the existing vegetation as well as those apparently dispersed from surrounding vegetation. Partridge suggests following disturbance within forest the soil seed bank will be a significant source of propagules to germinate immediately following disturbance, and that it is possible for a markedly different vegetation to arise once present cover is removed.

Given the differential composition of soil seed banks compared with current vegetation (Partridge 1989), and the observations of Burrows (summarised in Table 5.7), it is likely that at least some seeds present in the soil seed bank will germinate each year and that these seedlings may include species different to those present in the vegetation at a site. This may have contributed further to the discontinuity in the seed rain→seedling stage observed here. Soil seed banks in Hoon Hay Valley most certainly warrant further investigation, in terms of both their species composition and the rates and timing of germination from them such that the influence that they have on seedling recruitment may be more effectively enumerated.

iii. Vegetation → Seedlings

The strongest relationship in spatial pattern of all the ordinations compared is that between seedling pattern and current vegetation ($R^2 = 0.50$, Table 6.7). In spite of the large discontinuities in spatial pattern between vegetation and seed rain, and seed rain and seedling pattern, the spatial pattern of seedling populations is still most strongly related to the vegetation already present in the Valley. It is however a relatively weak

relationship, as an $R^2 = 0.50$ indicates that the derived relationship is only explaining ca. 50% of the observed variation in the data (ter Braak and Looman 1987, Ott and Mendenhall 1985).

Few studies have investigated recruitment processes in a integrated manner similar to that used in this study, and those few have generally observed similar discontinuities to those observed here. In an elegant and detailed study Herrera *et al.* (1994) observed significant discontinuities in spatial patterns of vegetation and seedling recruitment primarily as a result of discontinuities at the seed rain to seedling stage, similar to those reported here. The approach used by Herrera *et al.* (1994) however differed significantly from that used in this study. They adopted a probabilistic survivorship strategy for investigating the recruitment processes of a single species, rather than relating recruitment to overall community-level patterns. As shown in Table 6.5 the response of individual species can differ markedly and so conclusions drawn from study of one species may differ substantially from those drawn from study of another.

The discontinuities observed by Herrera *et al.* (1994) occurred primarily at the seedling stage, and the authors partially explain this with reference to Collins (1989), who observed that initial correlations between spatial vegetation and seedling patterns can disintegrate as seedlings mature. However close examination of Collins (1989) suggests otherwise, and that in fact the reverse is true. Collins (1989) suggests that as seedlings mature they develop vegetation that is more similar to that which was present at the time they germinated, and so presumably as seedlings age the spatial concordance between their patterns and patterns of vegetation increase. Given that the present study counted seedlings based on stature rather than presumed seedling age, the observation that spatial patterns exhibited the strongest coupling at the vegetation→seedling stage is consistent with Collins' observation. As some of the seedlings counted were possibly of advanced age coupling of spatial patterns will be influenced by the age-specific relationships observed by Collins (1989).

The species-level relationship observed by Herrera et al. (1994) is supported by other studies. For example Collins and Good (1987a) investigated the seedling regeneration niche (defined by them in relation to the Plant Niche concept of Grubb (1977)) for six species in remnants of oak-pine forest in New Jersey. They observed that seedling scale habitat differentiation can be quite species specific, and that different species can occupy different microhabitats over relatively small spatial scales. Similar results were found in a separate study (Collins and Good 1987b), in which it was suggested that species-level habitat differentiation may be due to abiotic factors brought about by differing canopy composition. These may explain in part the difference in result between the community level result of the current study and that species-level result of Herrera *et al.* (1994).

More importantly the observation of Collins and Good (1987a, 1987b) help explain the observation that habitat-level coupling is generally always weaker than coupling at the overall level.

The reductionist approach of Herrera *et al.* (1994) is invaluable for enumerating those factors which are exerting the greatest influence on coupling of recruitment at the species level, and Herrera *et al.* (1994) make some particularly important observations which the results presented here readily support. They observed the importance of actions at the disperser stage, with seed deposition having a lasting impact on the recruitment of the species they studied. This is particularly significant when considering the dispersal coupling relationships observed in Table 6.7 and the significant between habitat-type differences in seed rain of Chapter 4. However they had as their main conclusion the observation that "later acting factors in the recruitment process have a definite potential to obscure or even cancel the effects of earlier ones, thus leading to a serious disruption of the [recruitment] process and a reduction in the overall predictability of its demographic consequences." (Herrera *et al.* 1994, p. 340) They state that this overall breakdown in predictability is a reflection of the breakdown in coupling of the individual stages, and that from the viewpoint of the parent plant this loss of predictability represent a significant loss of control over the recruitment process.

However the results presented here are for uncoupling at the community level, and in this respect they have significant implications for processes of succession and vegetation change. Previous studies (Williams 1983) have indicated that Hoon Hay Valley is a dynamic successional environment, with successional processes proceeding with some vigour (see Chapter 3 for a more detailed discussion of this). The observed discontinuities in spatial coupling of recruitment processes indicate a strong potential for vegetation change in the Valley; the future vegetation, represented by seed and seedling populations, will be different from that currently in the Valley, reaffirming the dynamic successional nature of the Valley vegetation.

One of the most significant observations of the current study is the consistently significant differences between habitat types for virtually all the attributes measured, both at the overall level and for individual species. The coupling of recruitment processes (Table 6.7) is always strongest when viewed at the overall level, indicating that uncoupling is most strongly expressed at the habitat level. This has particular relevance for vegetation change, particularly when considering processes of within-Valley colonisation and species migration. A consistent theme of discussion in Chapters 4 and 5 is that dispersal confers significant benefits to plant species, particularly in dynamic successional environments (Harper 1977, Burrows 1990, Gelnn-Lewin and van der Maarel 1992). Given the strong discontinuities at the vegetation→seed rain and the seed

rain→seedling stages it is readily apparent that significant dispersal is occurring. The observation that coupling is always weakest at the habitat-level indicates that dispersal is occurring between habitats in a process of within-Valley migration. The importance of dispersal at this level to vegetation change is emphasised by Matlack (1994), who observed that processes at the dispersal stage had significant effects on species migration patterns. It is interesting to note that Matlack (1994) observed significant dispersal mode differences in recruitment success similar to the trend observed here (Table 6.5, 6.6).

Processes of vegetation change within the Valley can be considered at the habitat-type level with considerable reward. On the basis of previous research (Williams 1983) habitat types in the Valley were defined as a successional continuum from presumably immature scrub types to successively more mature forest vegetation (S1→S2→F1→F2). As described in Table 6.7 coupling of recruitment within each of these is different, and different from the coupling observed when processes are considered at the overall level. This habitat-specific coupling is directly related to processes of succession and migration.

Data presented in Chapter 3 through 5 indicate that processes of dispersal and succession are directly related to presumed successional maturity. Table 3.4 indicates that vegetation species diversity is directly related to successional stage, as diversity is significantly higher in more mature forest habitat types (F1 and F2) than in less mature scrub habitat types. Table 4.3 shows that the most abundant and diverse seed rain is experienced in the least diverse and mature habitat type (S2) and this is a direct indication that species are being dispersed within the Valley from more mature vegetation to habitat types earlier on the successional pathway.

This is confirmed by Tables 6.2, 6.3, and 6.4, which indicate that the largest uncoupling of spatial patterns is expressed at the level of the individual habitat types. Dispersal is uncoupling spatial patterns at the seed (Table 6.2) and seedling (Table 6.3) stage and providing impetus for vegetation change within the Valley. That these significant between-habitat type differences are not being expressed at the seedling stage (Table 5.5), and that uncoupling is weakest at the vegetation→seedling stage indicate that factors determining spatial patterns of seedling survival described in Chapter 5 are the most significant hindrances to within-Valley species migration and successional change.

c. Implications for restoration

This has significant implications for the ecological restoration of Hoon Hay Valley. As described in Chapter 1 management of ecosystems for restoration spans a continuum from minimum intervention to complete rebuilding of ecosystem structure and function. Management of the restoration of Hoon Hay Valley currently falls at the minimum intervention end of the restoration continuum, and until very recently restoration was

even less than that with the presence of browsing mammals creating significant impediments to the successful regeneration of vegetation. It is apparent that once browsing stock have been removed the trend of vegetation change on the Port Hills is away from pasture and, once a canopy has established over grass cover, toward natural forest (Lord 1991, Wilson 1994, Reay 1996, Partridge 1992). The successional trend within Hoon Hay Valley is in support of this.

The potential benefits of returning natural forest to the Port Hills are beginning to be widely recognised. Active restoration planting has been undertaken for some time at Kennedy's Bush immediately to the south of Hoon Hay Valley, and Reay (1996) investigated the success of these. The restoration plantings at Kennedy's Bush are dominated by dense even aged monospecific stands of *Olearia paniculata*, which is a species not usually important in Port Hills successional vegetation. Indeed the individuals planted are from a non- Banks Peninsula provenance, and this has been seen by some to be a significant negative factor in Kennedy's Bush restoration. Reay (1996) found that this is not in fact the case. Far from being a negative influence the plantings of *Olearia* were enhancing natural processes of regeneration, and significantly shortening the amount of time needed for succession from bare pasture to native forest. Even though *Olearia* is not thought to be a significant attractant for bird dispersers, recruitment of bird dispersed seedling species beneath *Olearia* plantings was similar to that beneath natural forest at Ahuriri Bush (Reay 1996). Reay concludes that the species initially used in restoration planting at Kennedy's Bush do not greatly influence the outcome of restoration. This indicates that once pasture is overtopped by woody species regeneration toward native forest will proceed apace, irrespective of initial vegetation cover.

The results presented here for Hoon Hay Valley support this conclusion. Successional vegetation in Hoon Hay Valley has a significant component of introduced species (both plant and animal; see Chapter 3, Appendix 1 and 2, Williams 1983), and it is clear from the strong successional trend indicated by uncoupling of spatial patterns that these are not having an adverse effect on processes of regeneration to native forest. Many of these species are in other situations regarded as weeds, but their importance in Valley successional processes cannot be overemphasised. There is growing recognition of the importance of non-native species in succession to native forest (e.g. Williams 1983, Wilson 1994), and the results presented here certainly support this.

Indeed it is interesting to note that the brushtail possum (*Trichosorus vulpecula*), an introduced animal species widely recognised to have significant adverse effects on New Zealand's forested areas, may in fact be having a significant positive effect on the restoration of Valley vegetation. As Table 4.8 indicates possums dispersed ca. 16% of

the total Valley whole seed rain. While the fate of these seeds was not addressed (although it is the subject of current research), it is clear that possums may be having a positive effect on succession in terms of seed dispersal. Concurrent research (O'Cain 1997) has indicated that as possum numbers in the Valley are quite low the positive effects of possum seed dispersal may not be outweighed by negative effects of possum herbivory. This is most certainly deserving of more integrated investigation.

It is apparent that the strongest impediments to rapid vegetation change in the Valley are occurring at the seedling stage, and in order to maximise natural regeneration and achieve restoration of the Valley vegetation the effect of these impediments will have to be reduced. This supports the general assertion of Wilson (1994) that with removal of causes of seedling mortality (in that case browsing mammals) regeneration of native woody vegetation on Banks Peninsula and the Port Hills is vigorous. Wilson's observations of regeneration at Hinewai on Banks Peninsula offer valuable comparisons with this study. In a diverse mosaic of successional vegetation similar to that found in Hoon Hay Valley all vegetation types are in an apparently strong successional trend toward forest dominated by native woody species. Wilson suggests that the exact successional pathway is different depending on which species establish immediately after disturbance, but the strong trend toward 'native' forest observed at Hinewai confirms the trends observed by Reay (1996) and those of this study.

Wilson offers other useful insights into enhancing restoration in areas already dominated by successional vegetation. Hinewai Reserve is managed using a philosophy of minimum intervention; the aim is to remove obvious impediments to natural regeneration, particularly introduced mammals and fire, and otherwise allows natural processes to proceed unchecked (Wilson 1994). Much of the day-to-day restoration work at Hinewai Reserve is involved in meeting clear boundary requirements of the Noxious Plants Act, improving fire precautions, track maintenance, and checking for the few introduced plants deemed deleterious to native regeneration (Wilson 1994). Other non-native plants are left essentially undisturbed, and Wilson observes that the single largest impediment to natural regeneration is the presence of introduced browsing mammals, and with removal of these from the Reserve natural regeneration is vigorous.

It is clear from comparison with Reay (1996) and Wilson (1994) that current restoration of Hoon Hay Valley is very much toward the minimum intervention end of the restoration spectrum. It is also clear that very little is required to facilitate restoration in environments such as Hoon Hay Valley, and that once initiated regeneration can be vigorous, even in the face of browsing pressure from feral stock and other introduced browsing mammals. Even though the greatest impediments to successful regeneration occur at the seed→seedling stage, the general uncoupling of spatial patterns indicate that

these are not having an overwhelmingly negative impact on the natural processes of regeneration. Provided that no significant impediments to regeneration emerge, the vegetation cover of Hoon Hay Valley will return to one dominated by native woody species.

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Colin Burrows gave names to most of the unidentified seeds I came across, and without his speedy and expert help seed identification would have been a tricky exercise indeed.

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Collecting data involved rather a lot of tedious work, as it does for any thesis, and so anything which makes the tedious boring bits more interesting is certainly welcome, so thanks to Marty, Margaret, Steve R, and Steve C for funtimes during seed counting. Who would have thought that filling rubber lab gloves with water and then freezing them in rude and amusing shapes could be so entertaining.

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If we shadows have offended
Think but this and all is mended,
That you have but slumber'd here
While these visions did appear.
And this weak and idle theme,
No more yielding but a dream,
Gentles, do not reprehend:
If you pardon we will mend.
And, as I am but an honest Puck,
If we have unearned luck
Now to 'scape the serpents tongue,
We will make amends ere long:
Else the Puck a liar call.
So, goodnight until you all.

William Shakespeare

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APPENDIX 1

HOON HAY VALLEY VASCULAR PLANT CHECK LIST

From personal observation, herbarium collection of M. O'Cain, and Wilson (1993).
+ denotes adventive species.

1. Trees and shrubs

Alectryon excelsus (Sapindaceae)	Titioki
Aristotelia serrata (Elaeocarpaceae)	Makomako, wineberry
Brachyglottis sciadophila (Asteraceae)	
Carmichaelia 'common' (Fabaceae)	native broom
Coprosma spp. (Rubiaceae)	
C. areolata	
C. crassifolia	mikimiki
C. linarifolia	
C. propinqua	mikimiki
C. propinqua x *robusta*	
C. rhamnoides	mikimiki
C. robusta	karamu
C. rotundifolia	
C. virescens	mikimiki
Cordyline australis (Asteliaceae)	cabbage tree
Dodonaea viscosa (Sapinadaceae)	akeake
Fuchsia excorticata (Onagraceae)	kotukutuku
Griselinia littoralis (Grisiliniaceae)	broadleaf
Hebe strictissima (Scrophulariaceae)	
Helichrysum lanceolatum (Asteraceae)	niniao
Hoheria spp. (Malvaceae)	lacebark
H. angustifolia	
H. populnea var. *lanceolata*	
Ileostylus micranthus (Loranthaceae)	mistletoe
Kunzea ericoides (Myrtaceae)	kanuka
Lophomyrtus obcordata (Myrtaceae)	rohutu
Melicope simplex (Rhamnaceae)	poataniwha
Melicytus ramiflorus (Violoaceae)	mahoe
Myoporum laetum (Myoporaceae)	ngaio
Myrsine spp. (Myrsinaceae)	mapou
M. australis	

M. divaricata	
Olearia paniculata (Oleaceae)	akiraho
Pennantia corymbosa (Icacinaceae)	kaikomako
Pittosporum spp. (Pittosporaceae)	
P. eugenioides	lemonwood, tarata
P. tenuifolium	kohuhu
Plagianthus regius (Malvaceae)	lowland ribbonwood
Podocarpus spp. (Podocarpaceae)	
P. halii	thin-barked totara
P. totara	totara
Prumnopitys taxifolia (Podocarpaceae)	matai
Pseudopanax spp. (Araliaceae)	
P. arboreus	fivefinger
P. crassifolius	lancewood
Pseudowinter colorata (Winteraceae)	horopito
Schlefflera digitata (Araliaceae)	sevenfinger, pate
Solanum laciniatum (Solanaceae)	poroporo
Sophora microphylla (Fabaceae)	kowhai
Streblus heterophyllus (Moraceae)	milk tree
Urtica ferox (Urticaceae)	ongaonga
+*Acer psuedoplatanus*	sycamore
+*Crataegus monogyna*	hawthorn
+*Cytisus scoparius*	broom
+*Euonymus europaeus*	spindleberry
+*Pinus radiata*	
+*Prunus* spp.	
P. avius	cherry
P. cerasifera	cherry plum
+*Ribes sanguineum*	flowering currant
+*Rosa rubiginosa*	sweet brier
+*Salix fragilis*	crack willow
+*Sambuccus nigra*	elder
+*Ulex europaeus*	gorse

2. Climbers and Scramblers

Calystegia tuguriorum (Convolvulaceae)	native bindweed
Clematis foetida (Ranunculaceae)	

Fuchsia perscandens (Onagraceae)	climbing fuchsia
Muehlenbeckia spp. (Polygonaceae)	pohuehue
M. australis	
M. complexa	
Parsonsia spp. (Apocynaceae)	native jasmine
P. capsularis	
P. heterophylla	
Pasiflora tetrandra (Passifloraceae)	native passion vine
Ripogonum scandens (Ripogonaceae)	suplejack
Rubus spp. (Rubiaceae)	
R. cissoides	
R. schmidelioides	
R. schmidelioides x *squarrosus*	
R. squarrosus	
+*Lonicera japonica*	japanese honeysuckle
+*Leycesteria formosa*	Himalayan honeysuckle
+*Rubus fruticosus* agg.	blackberry
+*Solanum dulcamara*	bittersweet

3. Ferns and Fern Allies

Asplenium spp.
- *A. bulbiferum* subsp. *gracillimum*
- *A. flabellifolium*
- *A. hookerianum*
- *A. terrestre*

Blechnum fluviatile
Hypolepis rufobarata
Pellaea rotundifolia
Phymatosorus pustulatus
Polystichum richardii
Pteridium esculentum

4. Herbaceous Dicotyledons

Acaena spp.
- *A. anserinifolia*
- *A. novae-zelandiae*

Cardamine debilis

Crassula sieberiana
Galium propinquum
Gnaphalium spp.
    G. dudax
    G. involucratum
Haloragis erecta
Hydrocotyle spp.
    H. heteromeria
    H. elongata
    H. moschata
Leptinella squalida subsp. *mediana*
Oxalis exilis
Pseudognaphalium luteo-album
Ranunculus reflexus
Senecio spp.
    S. glomeratus
    S. minimus
Stellaria decipiens
Urtica incisa
Wahlenbergia gracilis

+*Anagallis arvensis*
+*Anthriscus caucalis*
+*Aphanes inexpectatus*
+*Callitriche stagnalis*
+*Cardamine hirsuta*
+*Carduus* spp.
    C. pycnocephalus
    C. tenuiflorus
+*Cerastium* spp.
    C. fontanum subsp. *vulgare*
    C. glomeratum
+*Cirsium* spp.
    C. arvense
    C. vulgare
+*Conium maculatum*
+*Conyza albida*
+*Crepis Capillaris*

+*Digitalis purpurea*
+*Epilobium ciliatum*
+*Erodium cicutarium*
+*Euphoria peplus*
+*Galium aparine*
+*Geranium* spp.
    G. dissectum
    G. molle
+*Lactuca serriola*
+*Marrubium vulgare*
+*Medicago lupulina*
+*Mycelis muralis*
+*Nepeta catoria*
+*Ranunculus* spp.
    R. parviflorus
    R. repens
+*Rumex* spp.
    R. crispus
    R. pulcher
+*Sherardia arvensis*
+*Silybum marianum*
+*Sisymbrium officinale*
+*Solanum nigrum*
+*Sonchus* spp.
    S. asper
    S. oleraceus
+*Stellaria media*
+*Taraxacum officinale*
+*Trifolium* spp.
    T. dubium
    T. glomeratum
    T. repens
    T. subterraneum
+*Urtica urens*
+*Verbascum thaspus*
+*Veronica arvensis*
+*Vicia sativa*

5. Herbaceous monocotyledons

Astelia fragrans
Carex spp.
    C. forsteri
    C. solandri
    C. virgata
Dichelachne crinita
Echinopogin ovatus
Elymus rectisetus
Juncus spp.
    J. distegus
    J. gregiflorus
Lachnagrostis richardii
Libertis ixioides
Microlaena spp.
    M. polynoda
    M. stipoides
Poa spp.
    P. cita
    P. imbecilla
    P. matthewsii
Pterostylis spp.
    P. areolata
    P. graminea
Rytidosperma unarede
Uncinia leptostachya

+*Agropyron repens*
+*Agrostis* spp.
    A. capillaris
    A. stolonifera
+*Alopecurus geniculatus*
+*Anthoxanthum odoratum*
+*Bromus* spp.
    B. diandrus
    B. hordaceus
+*Cynosurus* spp.
    C. cristatus

C. echinatus
+*Dactylis glomerata*
+*Glyceria declinata*
+*Holcus lanatus*
+*Hordeum leporinum*
+*Juncus* spp.
J. bufonis
J. filicaulis
+*Lolium perenne*
+*Poa pratensis*
+*Vulpia bromoides*

APPENDIX 2

1. Hoon Hay Valley Avifauna

List based on personal observation, also Wilson (1993)
Nomenclature follows Heather and Robertson (1996)

Acanthizidae	
Gerygine igata	Grey Warbler
Accipitridae/Falconidae	
Circus approximans	Harrier
Alaudidae	
Alauda arvensis	Skylark
Anatidae	
Anas platyrhynchos	Mallard duck
Anas supercilliosa	Grey duck
Tadorna variegata	Paradise duck
Ardeidae	
Ardea novaehollandiae	White faced heron
Columbidae	
Hemiphaga novaeseelandiae	Kereru
Columba livia	Rock Pigeon
Cracticidae	
Gymnorhina tibicen	Australian Magpie
Cuculidae	
Chrysococcyx lucidus	Shining cuckoo
Emberizidae	
Emberiza citrinella	Yellowhammer
Eopsaltriidae	
Petroica macrocephala	Tomtit
Fringillidae	
Fringilla coelabs	Chaffinch
Carduelis flammea	Redpoll
Carduelis chloris	Greenfinch
Carduelis carduelis	Goldfinch
Meliphagidae	
Anthornis melanura	Bellbird
Monarchidae	
Rhipidura fuliginosa	Fantail
Muscipidae	

Turdus merula	Blackbird
Turdus philomelos	Songthrush
Phasianidae	
Callipepla californica	Californian quail
Ploceidae	
Passer domesticus	House sparrow
Sturnidae	
Sturnus vulgaris	Starling
Zosteropidae	
Zosterops lateralis	Silvereye

2. Hoon Hay Valley Mammal Fauna

List of mammals currently in Valley, or present recently. Based on personal observation, Wilson (1993), and communication with John Sheridan, Valley resident. Nomenclature follows King (1990).

Cervidae	
Cervus elaphus	Red deer
Felidae	
Felis catus	Feral cat
Leporidae	
Lepus europaeus occidentalis	Hare
Oryctolagus cuniculus	Rabbit
Muridae	
Mus musculus	Mouse
Rattus rattus	Ship rat
Mustelidae	
Mustela ermina	Stoat
Phalangeridae	
Trichosorus vulpecula	Brushtail possum
Suidae	
Capra hircus	Goat
Sus scrofa	Pig
Ovis aries	Sheep

APPENDIX 3

Six letter speceis codes used in tables and figures in Chapters 3, 4, and 5.

ACAANS	*Acaena anserinifolia*
ACASPP	*Acaena* spp.
ALEEXC	*Alectryon excelsus*
ANTODO	*Anthoxanthum odoratum*
ARISER	*Aristotelia serrata*
BETSPP	*Betula* spp.
BROSPP	*Bromus* spp.
CALTUG	*Calystegia turgoriorum*
CARSPP	*Carduus* spp.
CLEFOE	*Clematis foetida*
COPAER	*Coprosma aereolata*
COPLIN	*Coprosma linarifolia*
COPPRO	*Coprosma propinqua*
COPPXR	*Coprosma propinqua* x *robusta*
COPROB	*Coprosma robusta*
COPROT	*Coprosma rotundifolia*
COPVIR	*Coprosma virescens*
CRAMON	*Crataegus monogyna*
CYTSCO	*Cytisus scoparius*
DODVIS	*Dodonea viscosa*
EUOEUR	*Euonymus europaeus*
FUCEXC	*Fuchsia excorticata*
GRILIT	*Grisilinea littoralis*
HELAGG	*Helichrysum aggregatum*
HOHANG	*Hoheria angustifolia*
HOHSPP	*Hoheria* spp.
HYPRAD	*Hypochoeris radicata*
ILEMIC	*Ileostylus micranthus*
JUNSPP	*Juncus* spp.
KUNERI	*Kunzea ericoides*
LEYFOR	*Leycesteria formosa*
MELRAM	*Melicytus ramiflorus*
MELSIM	*Melicope simplex*
MEUAUS	*Muehlenbeckia australis*
MEUCOM	*Muehlenbeckia complexa*
MYOLAE	*Myoporum laetum*

MYRDIV	*Myrsine divaricata*
PARCAP	*Parsonsia capsularis*
PARHET	*Parsonsia heterophylla*
PARSPP	*Parsonsia* spp.
PENCOR	*Pennantia corymbosa*
PITEUG	*Pittosporum eugenoides*
PITTEN	*Pittosporum tenuifolium*
PLAREG	*Plagianthus regius*
PRUAVI	*Prunus avium*
PSECOL	*Pseudowintera colorata*
PSESPP	*Pseudopanax* spp.
PSEARB	*Psuedopanax arboreus*
PSECRA	*Pseudopanax crassifolius*
PTEESC	*Pteridium esculentum*
RUBIDA	*Rubus idaeus*
RUBFRU	*Rubus fruticosa* agg.
RUBSPP	*Rubus* spp.
RUMSPP	*Rumex* spp.
SAMNIG	*Sambuccus nigra*
SCHDIG	*Schlefflera digitata*
SOLDUL	*Solanum dulcemera*
SOPMIC	*Sophora microphylla*
ULEEUR	*Ulex europaeus*
URTFER	*Urtica ferox*
UNCLEP	*Uncinnia leptostachya*
VICSPP	*Vicea* spp.